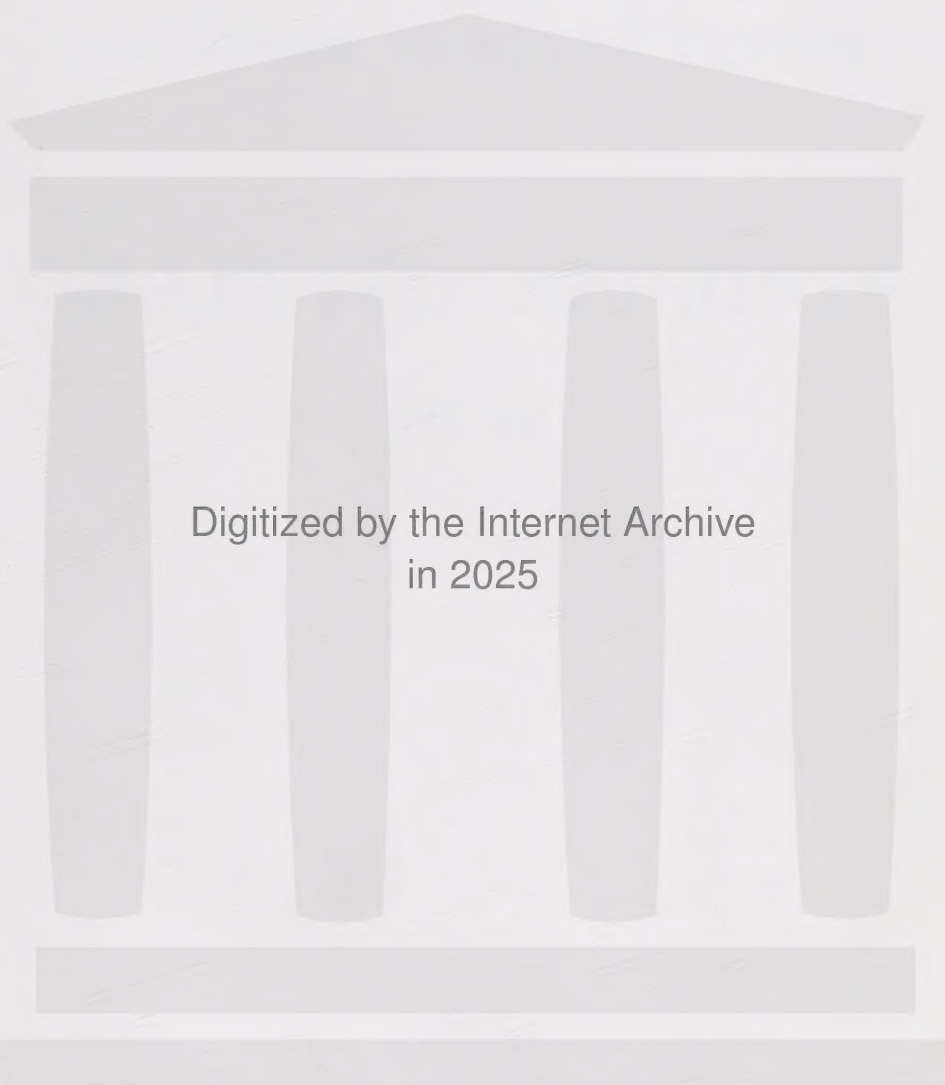


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TABLE OF CONTENTS

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DETERMINATION OF SURFACE DRIFT PATTERNS AFFECTING
FISH STOCKS IN THE CALIFORNIA CURRENT UPWELLING REGION

by

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Abstract

Surface marine observations are used to infer the large-scale seasonal patterns of ocean surface drift near the coast in the California Current. Striking conformities are noted between these patterns and regional faunal groupings. In the Pacific Northwest coastal fish species having pelagic larvae tend to spawn during the winter season when surface wind drift is generally directed toward the coast, rather than during the more productive upwelling season. In the region of vigorous upwelling off Northern California, which is characterized by strong offshore surface transport through most of the year, there is a paucity of locally spawning species. Rather, the fish stocks which harvest the massive productivity of that region are mainly migrating species which spawn under the more favorable drift conditions of the Southern California Bight. Closed gyral circulations in the Southern California Bight and off southern Baja California appear to foster favorable spawning conditions, leading to distinct faunal assemblages.

The apparent dependence of spawning strategies upon surface drift conditions suggests the hypothesis that anomalies in surface drift patterns could be a cause of the observed wide variations in spawning success of the major fishery species of the California Current region. Geostrophic currents tend to parallel coastal boundaries; thus a reasonable assumption is that major anomalies in the onshore-offshore component of surface transport are related to fluctuations in the surface wind drift. Indices of surface Ekman flux are derived from wind reports from ships at sea.

Other biologically important index series can be derived from related information. Offshore-directed surface Ekman flux can be linked to locally wind-induced coastal upwelling. Ekman flux divergence offshore of the coastal boundary zone may control concentration or dispersion of fish larvae, food organisms, and predator organisms. Wind mixing energy added to the water column can destroy vertical stratification of food particles, thought to be important to survival of first feeding fish larvae. Such index series have been applied to studies of the variations of such stocks as Pacific mackerel, Dungeness crab, English and Dover soles, northern anchovy, rockfish and Atlantic menhaden.

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Introduction

The California Current is a highly productive upwelling system, containing important fishery resources. The coastal fisheries have historically been subject to extreme fluctuations which have resulted in economic hardships. The Pacific sardine fishery expanded rapidly in the early 1930's to become the region's most important fishery, with 774,000 MT landed in the 1936-37 season. Thereafter the stocks declined to the point that the fishery had virtually disappeared by the late 1960's. Similarly, Pacific mackerel landings reached a peak of 66,500 MT in 1935-36, only to decline to a level near 1,100 MT by 1969. Estimates of northern anchovy spawning biomass off Southern California indicate an explosive increase from 267,000 MT in 1951 to 5,635,000 MT in 1965 and a recent decline to 1,180,000 MT in 1978. The lack of obvious relationships between stock size and recruitment in these and other pelagic species indicates an important effect of environmental conditions on the viability of the stocks. Truly effective management of the fishery resources of the region will require a capability to predict and allow for the effects of environmental variability. Recently, some promising hypotheses have been formulated, and environmental index time series suitable for testing the hypotheses are being developed.

Surface Ekman transport

Winter and summer distributions of surface Ekman transport, computed from the wind stress summaries of Nelson (1977), are presented in Figures 1 and 2. In these presentations summaries of stress computations from each available surface wind observation in the surface marine observation file (TDF-11) were made for each one-degree areal quadrangle. Each vector symbol represents a discrete sample which is completely independent of every other sample. No spatial smoothing has been applied.

During the winter (Figure 1) Cape Mendocino marks a division between generally onshore-directed Ekman transport to the north and offshore-directed transport to the south. Strongest offshore transport occurs off central Baja California. During the summer (Figure 2) Ekman transport tends to be directed offshore throughout the region, most strongly from Cape Blanco to Point Conception. The Southern California Bight, south of Point Conception appears as a local minimum in offshore transport.

Since offshore Ekman flux is the primary driving force for locally wind induced coastal upwelling (Figure 3), the area south of Cape Mendocino is characterized by coastal upwelling throughout the year. To the north, there is a seasonal alternation, with coastal upwelling predominating in summer and downwelling predominating during winter.

In these presentations (Figures 1 and 2) spatial detail has been achieved by compositing all available data in a given season from a large number of years, basically on the grounds that seasonal variability in temperate latitudes is generally large compared to interyear variability. Such spatial

resolution is never available in a synoptic sampling (Figure 4). For most practical applications a time series of variations in transport is required. However in forming time series from sparse observations which are sporadically distributed in time and space, the variability introduced by random errors in measurement or by changes in spatial distribution of reports may be as large as the variability in the processes themselves. Some method of objective analysis which filters out the small scale variability is required to produce homogeneous time series. Well developed objective analysis techniques are routinely employed by meteorological agencies.

One approach to producing time series indicators of Ekman transport is Bakun's (1975) upwelling indices. These are computed from synoptic surface atmospheric pressure analyses generated at the U.S. Navy's Fleet Numerical Weather Central. Wind reports are included in these analyses as equivalent pressure gradients according to the "Fields by information blending" methodology (Holl and Mendenhall, 1972). A geostrophic approximation and a simplified treatment of the planetary boundary layer are used to estimate the sea surface stress and resulting Ekman transport (Bakun, 1973). The component of Ekman transport perpendicular to the coast is resolved, positive values indicating offshore transport and negative values indicating onshore transport. A one-year sample of daily means of the 6-hourly synoptic computations (Figure 5) illustrates the characteristic seasonal and shorter scale variability.

Off the coasts of the states of Washington and Oregon (48N and 45N latitudes) the seasonal pattern is dominated by short intense bursts of onshore Ekman flux caused by winter storms. The summer season exhibits much lower energy pulsations, chiefly in the offshore direction. Off the state of California (39N, 36N) the summer is characterized by intense bursts of upwelling-producing offshore transport; the winter season is a more equal mix of onshore and offshore transport events. Off the state of Baja California in Mexico (30N, 27N) a lower level but steadier succession of offshore transport pulses continues throughout the year; the maximum intensity of upwelling producing offshore Ekman flux tends to occur in the early spring rather than in the late spring and early summer as is the case further north. At all the locations a large amount of the variance occurs in the "atmospheric event" frequency range, encompassing periods from greater than a day to several weeks.

Reproductive Strategies of Fishes

On the large time and space scales involved in the larval drift of a fish stock, the surface flow field can be adequately viewed as being a linear combination of the geostrophic flow field and the surface drift caused by the stress of the wind on the sea surface. A satisfactory approximation to the surface wind drift is provided by the Ekman transport. The conceptual picture, then, is of a thin surface layer of Ekman drift which varies in phase with atmospheric weather patterns, superimposed on a deeper, more slowly varying geostrophic flow field (Parrish, Nelson and Bakun, manuscript). Geostrophic flow in the California Current tends to parallel the coast; in the Southern California Bight south of Pt. Conception a cyclonic gyral circulation exists most of the year (Reid, Roden and Wyllie, 1958). A similar cyclonic circulation

tends to occur off southern Baja California, south of Punta Eugenia (Bakun and Nelson, in press).

The flow patterns that can be inferred from the combined Ekman and geostrophic fields suggest that, for purposes of larval transport, the California Current system can be divided into four regions:

- (1) The Pacific Northwest region (north of Cape Blanco),
- (2) The region of maximum upwelling (Cape Blanco to Pt. Conception),
- (3) The Southern California Gyre (Pt. Conception to central Baja California),
- (4) The southern Baja California region.

The correspondence of the reproductive strategies of California Current fishes to this regional subdivision is striking.

(1) In the Pacific Northwest region, the surface Ekman drift is predominantly offshore during the summer upwelling season, and strongly onshore during the winter. Nearly all the dominant commercial Pacific Northwest fishes have a late winter spawning period. This is not the expected spawning period for a temperate fish fauna as it comes well before the maximum plankton blooms. In contrast most of the north Atlantic cold temperate fish fauna has short spawning periods coincident with the spring plankton blooms (Cushing, 1975). Evidently, in the Pacific Northwest the necessity for avoidance of loss of epipelagic eggs and larvae from the favorable near-coastal zone outweighs the necessity for high food availability. Another common adaptation for reducing larval loss in Pacific Northwest fishes is the avoidance of epipelagic eggs. A common example is the spawning of demersal eggs in protected inshore waters (e.g. herring, lingcod, cottids, and most of the other intertidal and littoral fishes of this region). Other strategies include livebearing (rockfishes and embiotocids), anadromous spawning (salmonids and osmerids), deep water spawning (pleuronectids and sablefish), and extensive migrations to areas of more favorable larval transport (hake, sardine, albacore).

(2) In the region of maximum upwelling, between Cape Blanco and Point Conception, Ekman transport is generally offshore, intensely so during the spring and summer. The adaptations to avoid larval loss found in the temperate component of the fauna are similar to those described for the Pacific Northwest. There is probably a continuous colonization of the upwelling region by larvae which are advected into the region from the Pacific northwest region. The subtropical component of the fish fauna in this region is principally composed of adults which use this region as a feeding ground, but do not spawn there (i.e. hake, sardine, bonito, white seabass, Pacific mackerel, and albacore). Very few coastal fishes have their center of abundance in the upwelling maxima region; bocaccio, Sebastes paucispinis, and chilepepper, Sebastes goodei, (both live bearers) appear to be the best examples. Apparently, coastal species with pelagic eggs and larvae have great difficulty in maintaining large resident populations in this region of strongest offshore transport and upwelling. Rather, the commercially important harvesters of the massive

organic production of this area are migrating species which spawn under the more favorable transport conditions of the Southern California Gyre.

(3) In the Southern California Gyre, south of Point Conception there is a local minimum of offshore Ekman transport near the coast at all seasons of the year. The geostrophic component of flow forms a closed gyre. The dominant pelagic fishes of the California Current System (i.e. those which have supported large fisheries) all spawn in this region. The adult sardine, hake, jack mackerel and Pacific mackerel migrate to the northward areas for feeding. The central stock of the northern anchovy, probably because of limited swimming ability due to their small size, remains principally within the Southern California Gyre.

(4) In the southern Baja California region a number of pelagic fishes have subpopulations which are distinct from those in the Southern California Bight. These include sardine (Clark 1947), Pacific mackerel (Roedel 1952) and northern anchovy (Vrooman and Smith 1971). In addition, a large tropical component appears in the fauna of this region due to northward warm water advection along the coast and proximity to the warm Gulf of California.

This general pattern of correspondence between reproduction strategies and ocean flow characteristic suggests that the necessity for minimization of offshore loss of reproductive products by seaward transport processes must have exerted a particularly strong control on the development of spawning characteristics. This in turn implies an important effect of transport conditions upon reproductive success, leading directly to the hypothesis that deviations from "normal" transport conditions, to which reproductive strategies are adapted, may be a cause of the very large recruitment variations observed in the coastal fisheries of the California Current.

A major problem in defining the environmental-biological relationships which are required to construct useful predictive models for fishery management is that there are generally available only very small time series samples with which to work. Fishery data characteristically yield one data point per year and the period over which the time series can be considered homogeneous does not normally exceed ten to twenty years. To sort out a multitude of possible environmental effects from a series with ten to twenty data points is a statistically impossible task. It is necessary therefore to either find the means to reduce the multitude of environmental factors to one, or at most several, indices of integrated environmental state, or to hope that one or perhaps two environmental factors will have such a dominant effect as to be discernible through the "noise level" generated by the other environmental effects not accounted for. The considerations presented above suggest that surface drift during the early egg and larval period may be such a dominant environmental factor for some of the major coastal fishery species of the California Current.

Wind stress curl

At a coastal boundary, the divergence in the surface Ekman transport is controlled by the offshore component, as indicated in Figure 3. In the open ocean, away from the vicinity of the boundary, Ekman divergence is controlled by the wind stress curl (Fofonoff, 1963). Positive wind stress curl induces Ekman divergence; negative curl induces convergence. Thus there are four possible combinations of convergence or divergence within a narrow coastal boundary zone and offshore of that zone (Figure 6). Certainly there could be a significant biological difference between the two coastal upwelling situations (types C and D in Figure 6). In the former (type C) there would be continued divergence and lower intensity upwelling offshore of the coastal upwelling zone. In the latter (type D), convergence and downwelling prevail offshore; formation of convergent surface fronts where organisms would tend to be concentrated would be favored. These could be areas either of good feeding success or of high vulnerability to predation.

There are no routine measurements of wind stress curl. However, since forming the curl of a vector field is a linear operation, the curl of a mean field should resemble the mean of the corresponding curl field. The curl fields (Figures 7 and 8) corresponding to the winter and summer stress fields (Figures 1 and 2) were computed by forming finite difference derivatives among neighboring one-degree squares (Nelson, 1977). Much of the smaller scale detail, particularly in the northern portion of the winter distribution (Figure 7) can be attributed to sampling errors which are amplified when derivatives are taken. However the coherent larger scale features are certainly significant, appearing consistently in Nelson's (1977) long term monthly fields.

Negative wind stress curl, or surface convergence, predominates in the offshore region throughout the year. From this offshore region, a lobe of negative wind stress curl extends shoreward to the central Baja California Coast between Punta Baja and Punta Eugenia. This feature appears consistently during all seasons of the year. In this same area of coast there is a consistent local maximum in the offshore Ekman Transport (Bakun and Nelson, in press). Thus the area from Punta Baja to Punta Eugenia represents a type "D" situation (Figure 6) with vigorous coastal upwelling coupled with convergence and downwelling offshore of the coastal upwelling zone.

To the north and south of this lobe of negative curl are regions of positive wind stress curl, or surface divergence, which extend from 100 to 300 km offshore. Particularly strong positive curl characterizes the Southern California Bight. This strong positive curl area expands northward, following the northward seasonal progression of coastal upwelling, to occupy virtually the entire coast during summer (type C, Figure 6).

During the spring upwelling maximum off Baja California, sea surface flow is parallel to the coast and strongly equatorward in response to the pressure gradients established by the upwelling of denser waters near shore. When the upwelling relaxes in the fall, the surface circulation tends to separate into semi-independent cyclonic gyres (Figure 9) in the regions of positive

wind stress curl. From Punta Baja to Punta Eugenia, where the curl is negative, flow remains equatorward along the coast (Bakun and Nelson, in press). Possible explanations for this correspondence of flow and wind curl patterns include (a) the existence of some approximate "Sverdrup balance" near the coast (Nelson, 1977), and (b) the effect of surface Ekman pumping whereby the pressure gradients set up between areas of surface convergence and divergence would induce geostrophic currents parallel to stress curl contours. This is a matter of ongoing research at our laboratory. In either case fluctuations in wind stress curl pattern would be related to variations in current pattern.

The lobe of negative curl which appears to separate the gyres of Figure 9, is located also at the separation between the Southern California Gyre and Southern Baja California faunal regions, discussed in the previous section. An example of the faunal separation is the existence of separate subpopulations of northern anchovy (Figure 10). It is possible that fluctuations in the strength of the negative curl lobe could influence exchanges between the central and southern anchovy populations.

There is a lack of sufficient data density (Figure 3) to resolve features of the size of the negative curl lobe in any synoptic sampling in order to form time series to test and utilize this possibility. Presently we are forced to rely on an untested assumption that the small scale features would fluctuate in the same general sense as the much larger scale which can be resolved by the available data (Bakun and Nelson, in press). Satellite systems, with wind stress sensors yielding the 50-km resolution designed for SEASAT-A would seem to allow us, for the first time, to view wind stress patterns on the same scale that they may actually affect fishery stocks.

Applications

Computed upwelling indices (Bakun 1973) which estimate the fluctuations in offshore Ekman transport, and offshore divergence indices (Bakun and Nelson, in press) which reflect variations in the large scale wind stress curl pattern, are beginning to be utilized in studies of California Current fishery stocks. A statistical model which explained less than twenty percent of the variance in Pacific mackerel recruitment was improved to explain seventy-eight percent of the variance (Figure 11) by the addition of two environmental variables, the upwelling index and offshore divergence index series in the vicinity of the negative curl lobe off Baja California (Parrish and MacCall, in press). Apparent relationships with upwelling index series have also been demonstrated for anchovy (Anon., 1978), Dungeness Crab (Peterson, 1973, Botsford and Wickham, 1975), Coho salmon (Gonsolus, 1978), English and Dover sole (Hayman, 1978), and rockfish (Parrish, et al., manuscript). A similar computation of the onshore Ekman transport near Cape Hatteras, accounted for nearly sixty percent of the variance from a fitted stock-recruitment curve for the Atlantic menhaden fishery (Nelson, Ingham and Schaaf, 1977).

Concluding remarks

In defining the effect of the environment on fishery stocks we must deal with a space-time continuum of processes; the necessary coverage is generally not available from research vessel operations. Recently, progress has been made using routinely-collected maritime data. Composite long term seasonal summaries of surface wind and ship drift observations have revealed features not resolvable in available synoptic samplings. Comparisons of these features to known biological features have motivated testable hypotheses. Consistent time series on the lower resolution scale that is available synoptically have been generated from analyzed meteorological fields. These have been used to test hypotheses and establish fishery-environmental relationships suitable for management purposes.

Important new findings on the sensitivity of pelagic fish stocks to the breaking up of fine-scale food strata by wind mixing during early larval feeding (Lasker, 1978) have not been discussed here. However, their application in fishery management will similarly require consistent time series indicators of the effect of wind acting on the sea surface.

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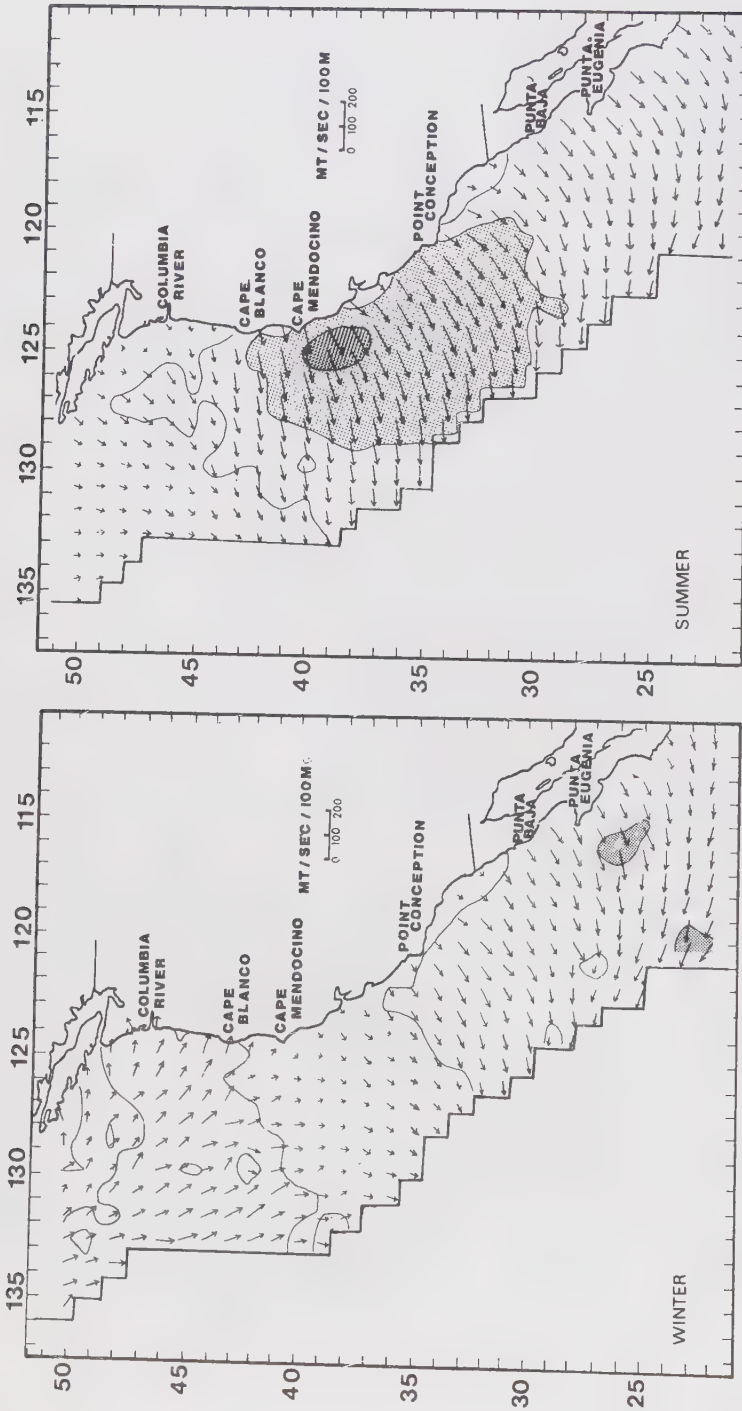


FIGURE 1. SURFACE EKMAN TRANSPORT DURING WINTER (DECEMBER THROUGH FEBRUARY LONG TERM 1° MEANS). CONTOUR INTERVAL IS 50 METRIC TONS PER SECOND ACROSS EACH 100 M WIDE. AREAS OF TRANSPORT GREATER THAN 100 MT/SEC/100 M ARE SHADED. STRESS ESTIMATES WERE COMPUTED FROM EACH AVAILABLE SURFACE WIND OBSERVATION AS THE PRODUCT OF THE SQUARE OF THE WIND SPEED, THE DENSITY OF AIR (CONSIDERED A CONSTANT EQUAL TO 0.00122 GM/CM³), AND A CONSIDERED A COEFFICIENT (0.0013) AND VECTORIALLY AVERAGED BY ONE-DEGREE "SQUARE" AREA. THE EKMAN TRANSPORT, DIRECTED NINETY DEGREES TO THE RIGHT OF THE MEAN STRESS, WAS CALCULATED BY DIVIDING BY THE LOCAL CORIOLIS PARAMETER.

FIGURE 2. SURFACE EKMAN TRANSPORT DURING SUMMER (JUNE THROUGH AUGUST LONG TERM 1° MEANS).

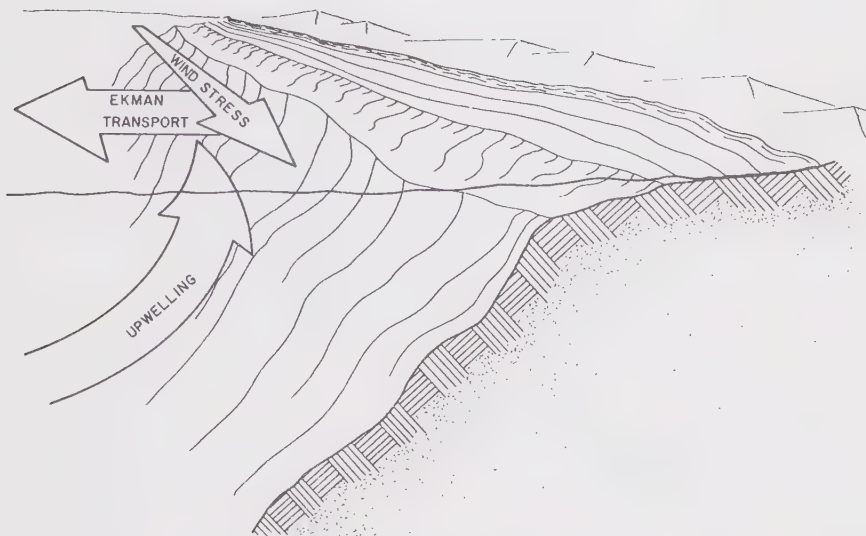


FIGURE 3. A CONCEPTUAL DIAGRAM FOR LOCALLY WIND INDUCED COASTAL UPWELLING. A COMPONENT OF WIND STRESS PARALLEL TO THE COAST AND DIRECTED EQUATORWARD INDUCES OFFSHORE TRANSPORT IN THE SURFACE EKMAN LAYER OF THE OCEAN. TO THE EXTENT THAT THIS OFFSHORE FLUX IS NOT BALANCED BY INFILUX OF HORIZONTAL SURFACE FLOW, THE BALANCE IS MAINTAINED BY UPWELLING OF DEEPER WATERS.

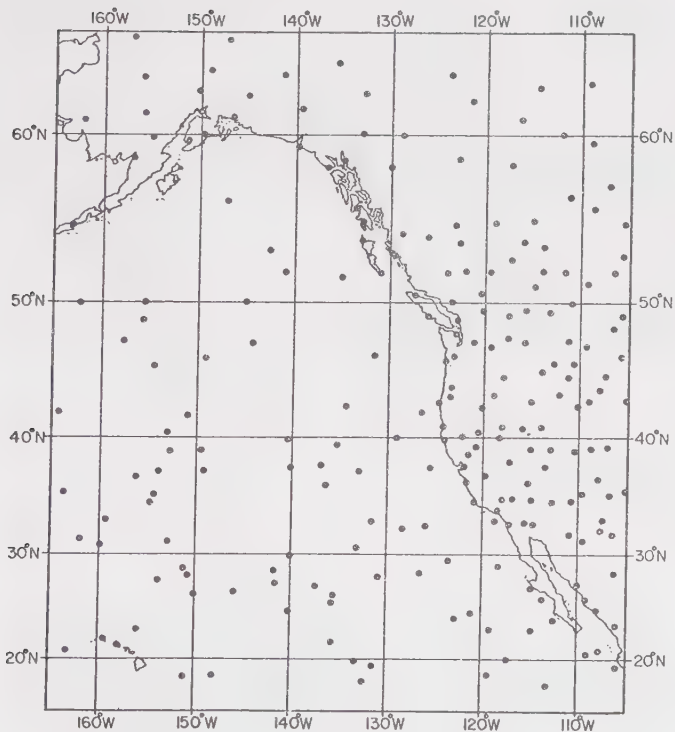


FIGURE 4. A TYPICAL DISTRIBUTION OF REPORTS AVAILABLE FOR A SYNOPTIC SURFACE ATMOSPHERIC WIND-PRESSURE ANALYSIS. THIS PARTICULAR DISTRIBUTION IS FOR 1800 GMT ON 5 JANUARY 1974.

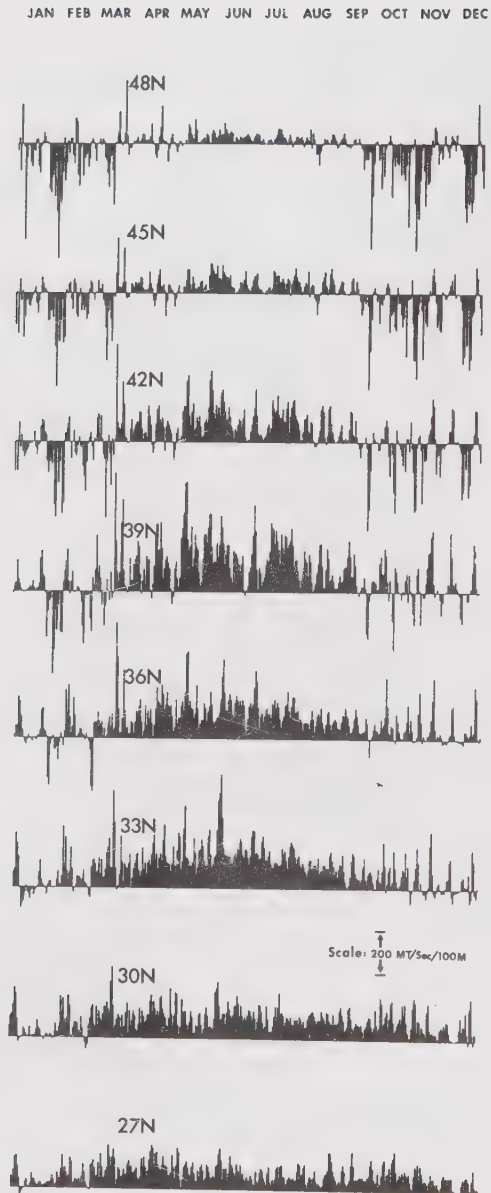


FIGURE 5. DAILY UPWELLING INDICES FOR 1975 AT 3-DEGREE INTERVALS FROM THE WASHINGTON COAST TO CENTRAL BAJA CALIFORNIA. THE MAGNITUDE OF THE ALONGSHORE WIND STRESS IS INDICATED BY THE LENGTH OF THE BARS; THE SCALE IS SHOWN ON THE FIGURE. UNITS ARE METRIC TONS PER SECOND PER 100 M LENGTH OF COAST. BARS EXTENDING UPWARD INDICATE SOUTHWARD STRESS EVENTS, WHICH CAUSE OFFSHORE EKMAN FLUX AND PRODUCE UPWELLING; THOSE EXTENDING DOWNWARD INDICATE SOUTHWARD STRESS EVENTS, WHICH PRODUCE ONSHORE EKMAN TRANSPORT AND RESULTANT COASTAL DOWNWELLING.

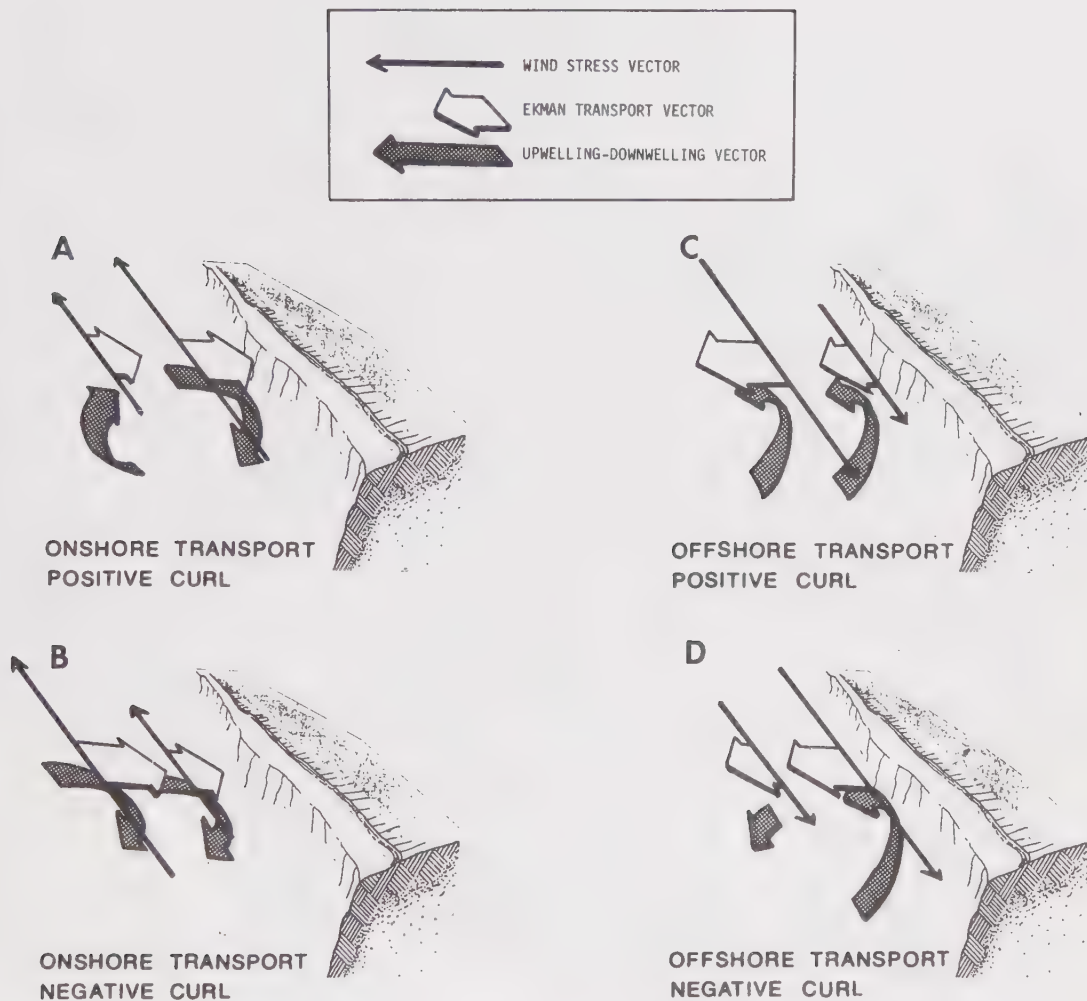


FIGURE 6. CLASSIFICATION OF WIND STRESS EVENTS ACCORDING TO COMBINATION OF COASTAL AND OFFSHORE CONVERGENCE OR DIVERGENCE. A. ONSHORE EKMAN TRANSPORT AND POSITIVE WIND STRESS CURL; CONVERGENCE AND DOWNWELLING AT THE COAST, DIVERGENCE AND UPWELLING OFFSHORE. B. ONSHORE EKMAN TRANSPORT AND NEGATIVE WIND STRESS CURL; CONVERGENCE AND DOWNWELLING AT THE COAST, CONTINUED CONVERGENCE OFFSHORE. C. OFFSHORE EKMAN TRANSPORT AND POSITIVE WIND STRESS CURL; DIVERGENCE AND UPWELLING AT THE COAST, CONTINUED DIVERGENCE OFFSHORE. D. OFFSHORE EKMAN TRANSPORT AND NEGATIVE WIND STRESS CURL; DIVERGENCE AND UPWELLING AT THE COAST, CONVERGENCE OFFSHORE.

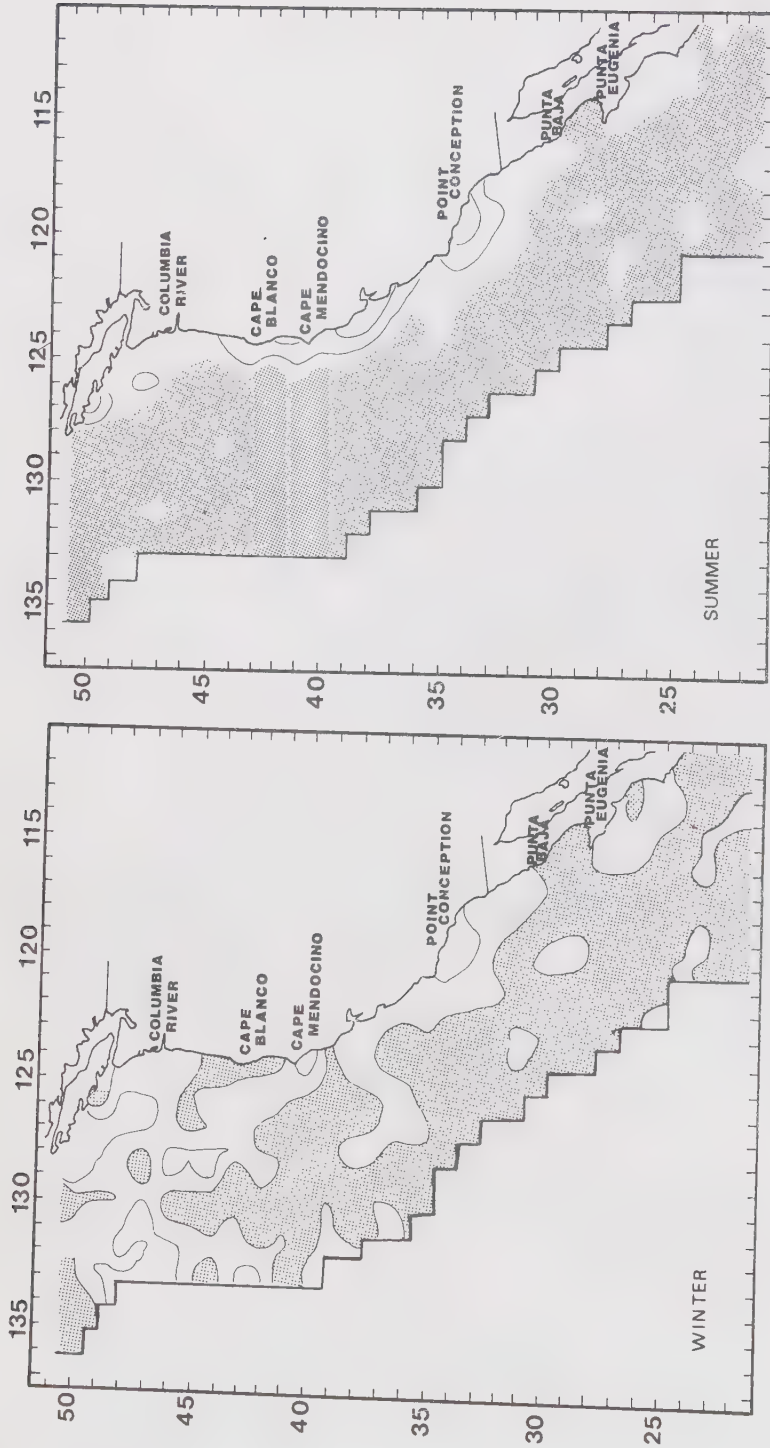


FIGURE 7. WIND STRESS CURL DISTRIBUTION DURING WINTER (DECEMBER THROUGH FEBRUARY LONG TERM MEANS). CONTOUR INTERVAL IS 0.25 DYNES CM⁻² PER 100 KM. NEGATIVE CURL VALUES ARE SHADED; I.E. SHADED AREAS INDICATE SURFACE EKVAN CONVERGENCE, UNSHADED AREAS INDICATE SURFACE DIVERGENCE.

FIGURE 8. WIND STRESS DISTRIBUTION DURING SUMMER (JUNE THROUGH AUGUST LONG TERM MEANS). CONVERGENT AREAS ARE SHADED; DIVERGENT AREAS ARE UNSHADED.



FIGURE 9. SHIP DRIFT DURING OCTOBER, NOVEMBER, AND DECEMBER. OBSERVATIONS WERE SUMMARIZED BY 2° "SQUARE" AREAS FROM THE NAVOCEANO SHIP DRIFT FILE. THE SMALL ARROWS, INDICATING MEAN DRIFT, ARE SCALED ACCORDING TO THE KEY AT THE LOWER LEFT. LARGE ARROWS SUGGEST THE INFERRED CIRCULATION PATTERN. SHIP DRIFT OBSERVATIONS ARE DERIVED FROM DIFFERENCES IN DEAD-RECKONING AND VERIFIED POSITIONS ASSEMBLED FROM SHIP'S LOGBOOKS.

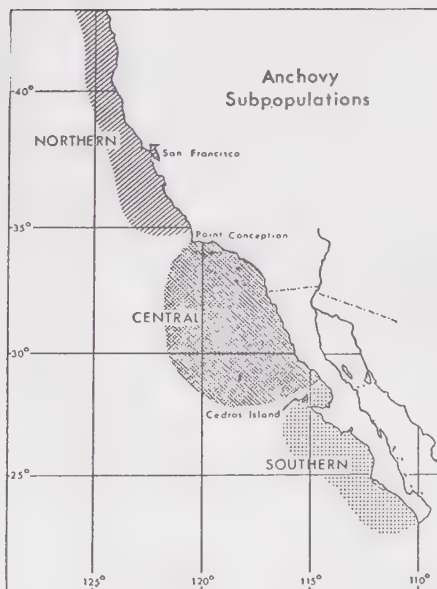


FIGURE 10. THE WINTER DISTRIBUTIONS OF ANCHOVIE SUBPOPULATIONS IN THE CALIFORNIA CURRENT (AFTER VROOMAN AND SMITH, 1971).

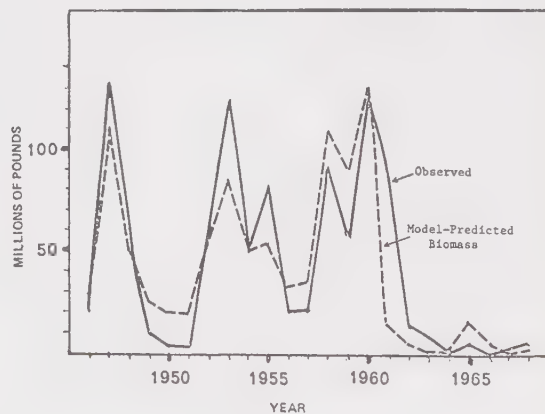


FIGURE 11. YEAR-CLASS SIZE IN THE CALIFORNIA STOCK OF PACIFIC MACKEREL.

Giant Larvacean Houses: Observations from Deep Submersibles

Eric G. Barham

Giant Larvacean Houses: Observations from Deep Submersibles

Abstract. *The abundance of large, previously unknown larvacean feeding structures in the deep ocean is a striking contrast to the rarity of such forms taken in net hauls. In some areas, abandoned houses and their disintegrated parts provide a substrate for other organisms and contribute to organic aggregates.*

Our concepts of oceanic mesopelagic life are mainly based on samples taken with trawls, nets, and pumps. However, new insights have been gained by underwater scuba divers in shallow oceanic waters; these observers report that several planktonic forms secrete mucoid feeding structures that are generally destroyed by our usual collecting methods (1).

The most elaborate of these structures are produced by larvaceans, urochordates that retain the larval tunicate "tadpole" anatomy. Minute (3 to 6 mm), shallow-dwelling species secrete cocoonlike mucous "houses" that are an order of magnitude larger than the animals and are equipped with intake screens and complex internal filters. Protectively situated in its house, the animal filter-feeds by creating a flow of water through the apparatus with its undulating tail. When the sieves clog, the larvacean evacuates the house and rapidly secretes another, a process that can be repeated at 2- to 4-hour intervals (2). Larvacean houses were studied by an earlier generation of biologists who carefully ladled these fragile structures from surface waters (3), but the abundance and importance of the abandoned houses as a substrate for microcrustaceans and bacteria and as a source of organic aggregates have only recently been revealed by modern diving techniques (2, 4).

Some 70 years ago, rare catches from deep net tows of *Bathochordaeus charon*, a larvacean more than ten times larger than shallow-dwelling forms, were reported (5). Recent examination of mid-water-trawl catches off the southern California coast has increased the known number of specimens of this giant form to 13 and extended their range to the eastern Pacific (6). Because the houses of *B. charon* have never been described

[Chun (3) theorized that they must be the size of pumpkins], I report here on observations made more than 10 years ago from deep submersibles (7).

My observations indicated that there are several types of large larvacean houses, ranging in size from 30 to 100 cm, that are widely distributed in pelagic waters adjacent to the continental shelves of the western middle American coast (Fig. 1). Their abundance varies from an occasional individual to one per cubic meter, a density observed above thermoclines at depths of 25 to 50 m. Some of my observations suggest that abandoned giant larvacean houses provide a substrate for microcrustaceans and contribute to organic particulate material in deep waters as do smaller forms at surface levels (2, 4).

During early dives, certain large mu-

cous structures seen from submersibles were an enigma to me. The evidence which eventually led me to conclude that these were extremely large larvacean houses follows. With the exception of their size, the structures were roughly similar to textbook descriptions of minute larvacean houses, and intact structures contained a double-lobed nucleus which resembled the internal filter of smaller forms. In some cases, a slow rhythmic beating by an organism adjacent to the nucleus appeared identical in position and motion to that described for minute larvacean forms. Once, a pollywog-shaped organism, about 6 to 8 cm in length, was seen leaving and swimming rapidly away from a disintegrating mucous structure that had been hit by the submersible. Finally, after several futile attempts, a structure containing an occupant was captured in a suction device attached to the front of the submersible (7). The collecting process reduced the structure to mucus-like scum; the organism, however, was recovered intact and examined in its fresh state by Donald P. Abbott (Stanford University) who identified it as a larvacean. (Unfortunately, this specimen was subsequently lost.)

While I recall seeing at least five types of large larvacean houses, by recourse to photographs and motion-picture films I can give general descriptions of three types. Type 1 house (Fig. 2A) is approximately 70 to 100 cm in its greatest dimension. The form of the house differs, but it is essentially a flimsy sac that appears to be at least partially open at the bottom. One or two mucous strings usually trail

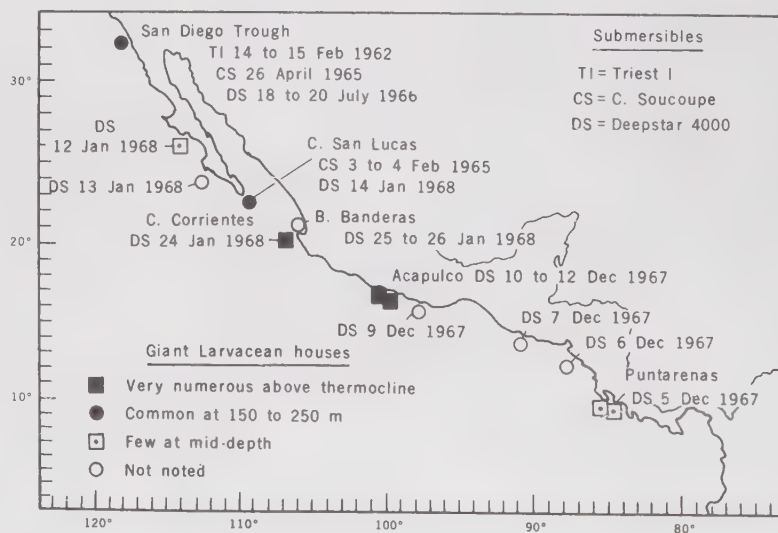


Fig. 1. Locations and dates of submersible dives and the observed relative abundance of large larvacean houses.

out of the bottom. The thin outer skin is covered with small particles. An internal filter, suspended by mucous strands, is situated in the upper region of the envelope. This filter is double-lobed, with a system of transverse ridges. When hit by the superstructure of a submersible, the house slowly disintegrates into ropy mucus. The type 2 house approximates an ovoid, about 20 to 26 cm in length. A double-lobed internal filter, larger in size relative to the envelope than that of type 1, is situated approximately in the middle of the house. The skin of the house appears firmer and is covered with fewer and larger particles than is type 1. What appears to be an external filter can be made out in one photograph (Fig. 2B). Type 3 house (Fig. 2C) is approximately a spheroid of about 30 to 40 cm in diameter. The outer skin is very flimsy, but strongly reflects light, apparently due to small adhered particles. The double-lobed internal filter is relatively large and centrally located. This type of house shatters into small pieces and fine particulate matter at the first contact with a submersible superstructure.

The type 1 house was noted on many dives off San Diego, California, the most detailed observations being made from

Deepstar 4000 (18 to 20 July 1966). During a four-dive series in the San Diego trough (Fig. 1) to depths of 600 to 700 m, some 60 type 1 houses were observed: 48 were seen at depths between 150 to 250 m; seven were above this level, the most shallow at 120 m; and five were below 250 m, the deepest at 375 m. Some houses were in various stages of disintegration, and on these houses small crustaceans (probably copepods) were resting on the outside and swimming around them. In another case, crustaceans were seen swimming away from a house and then returning to it. Crustaceans were also observed inside a disintegrating house clinging to and moving around on the internal filter. These observations were only possible when the submersible was motionless and the house was directly in front of the viewing port and sighted with a movable motion-picture light.

The type 2 house was observed and photographed from the *Cousteau Soucoupe* at about 120 m off Cabo San Lucas, Baja California, 4 February 1965 (Fig. 1). I cannot determine from my notes whether this specific type of house was observed on other dives.

In turbid, shallow water off Cabo Cor-

rientes, Mexico (Fig. 1), type 3 larvacean houses were so concentrated at 25 to 45 m that in some areas they were in contact with one another, but, on the average, there was about one house per cubic meter. Just below this concentration in a thin layer about 5 m deep, disintegrating houses formed what looked like a gelatinous matrix. Below this level to a depth of 70 m, there were about three internal filters per cubic meter. The houses and their disintegrating parts had apparently separated out on a strong thermal density gradient (the ocean temperature decreased some 9°C in the interval between 50 to 75 m). Below 75 m, I noticed only pieces of disintegrated houses, and these seemed to be smaller as we descended. At 130 m, small odd-shaped fragments could still be recognized as parts of houses. These were mixed with still smaller, spheroidal organic masses, 5 to 8 cm in diameter, considerably larger than the organic aggregates that are normally seen on submersible dives. Below 170 m, recognizable pieces of houses were no longer seen, but the relatively large organic masses were common. At greater depths, to 670 m, these masses appeared to have thinned, but still dominated the "marine snow." Deeper, when the submersible's lights were switched off, objects the size of these masses glowed with a bioluminescence suggestive of that produced by bacteria. Because of the observed orderly vertical transition, the masses may have been decomposing fragments of the houses.

On the ascent phase of the dive, I noted the same stratification of larvacean houses and their disintegrating parts. The isolated internal filters then appeared yellowish green in the increased ambient light, and I assumed that this was caused by phytoplankton that had clogged the filters. At 35 to 45 m I closely inspected a number of intact houses. In only about one out of eight cases could I detect signs of a live occupant, a ratio similar to that reported for small, shallow forms (2).

In two dives off Acapulco (Fig. 1), I had seen slightly fewer larvacean houses of the same type and the vertical stratification of disintegrating parts below their level of concentration was essentially the same. The Cape Corrientes and Acapulco dives were the only locations where so many houses were noted, and these aggregations are perhaps limited to productive nearshore tropical waters where currents and strong thermoclines interact as a concentrating mechanism. However, along a great expanse of the eastern Pacific, large larvaceans are much more common than is to be in-

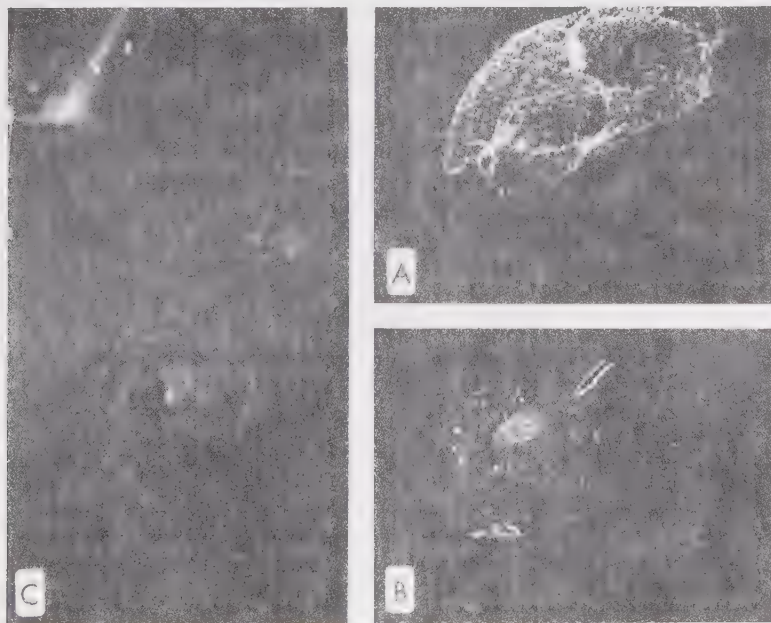


Fig. 2. Photographs of large larvacean houses taken during deep submersible dives. (A) Type 1 house, about 70 to 100 cm in its greatest dimension, at a depth of 200 m in the San Diego trough, 26 April 1965. (B) Type 2 houses, about 20 to 26 cm in length, at a depth of 120 m off Cabo San Lucas, Baja California, 4 February 1965. The arrow marks the probable intake filter. The organism below the house is a pelagic gastropod, probably *Pterotrachea coronata*. (C) The type 3 house at a depth of 40 m off Cape Corrientes, Mexico, 24 January 1968. The houses are about 30 to 40 cm in diameter and were disintegrating in the vortex caused by the submersible's movements. The bottom of the intake funnel of the collecting device (upper left) is 27 cm across. In all the houses the internal filters show clearly. The larvae, if present, should be closely associated with these structures although they cannot be made out in the pictures.

ferred from the few net-captured specimens. The obvious reason for this discrepancy between observations in situ and results from net hauls is the fragility of the houses (6), and perhaps that the unimposing preserved larvacean specimens are unrecognized in the gelatinous residues of net-haul samples

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5. C. Chun, *Aus den Tiefen des Weltmeeres* (Fischer, Jena, 1900), pp. 519-521.
6. C. P. Galt, *Fish. Bull.*, in press.
7. As part of the U.S. Navy Electronics Laboratory deep submersible program, the major objective of my dives was acoustic scattering studies. Observations were also made when there was the opportunity, and some of these and early attempts to collect large larvacean houses have been discussed [E. G. Barham, *Oceans Mag.* **1**, 55 (1968)]. The submersible vehicles have been described [R. F. Busby, *Manned Submersibles* (Office of Oceanographer of the Navy, Washington, D.C., 1976)]. I thank I. E. Davies, a fellow observer on many dives, who first pointed out the similarity between textbook figures and the then unidentified structures. The work from *Deepstar 4000* was aided by pilots R. P. Bradley and R. Church, both now deceased. Discussions with C. P. Galt, A. L. Shanks, and J. D. Trent have been helpful. In late 1966, N. B. Marshall suggested in correspondence that the largest type house could be that of *Bathochordaeus charon*.

21 March 1979, revised 28 June 1979

ANOMALIES OF MONTHLY MEAN SEA LEVEL ALONG THE WEST COASTS OF NORTH AND SOUTH AMERICA

Dale E. Bretschneider and Douglas R. McLain¹

INTRODUCTION

Measurements of mean sea level provide a source of long-term information concerning ocean processes. The data series of hourly tidal height measurements are unique among marine data series, in that they have been obtained inexpensively, over relatively long periods, at many fixed locations worldwide.

Many investigators have examined fluctuations of sea level at single stations, or relationships among small groups of stations. Roden (1960, 1963, 1966) used spectral and statistical methods to examine the interrelationships among sea level, temperature, and atmospheric pressure at selected stations along the west coast of North America. Saur (1972) examined sea level differences between the Hawaiian Islands and the California coast as an index of broad-scale changes in geostrophic flow in the California Current system. For fisheries assessment purposes, however, monitoring of ocean changes requires groups of stations covering larger areas. The stations examined in this report extend along the west coasts of North and South America from Massacre Bay, Attu, in the Aleutian Islands, to Caldera, Chile.

DATA

Most of the monthly mean sea level data in our data base were obtained from the University of Hawaii.² These data were updated

¹ Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93940.

² We thank K. Wyrski and B. Kilonsky, Department of Oceanography, University of Hawaii, who assembled these data and provided us with a tape copy.

and expanded with data from other sources.³ All data were converted to centimeters.

For this report, tide stations most representative of open ocean conditions were selected. Although many tide gage stations examined in this report are located on piers in sheltered coastal harbors, stations subject to highly variable local tidal conditions common to large river mouths (such as Astoria, OR), large shallow bays (such as Alameda, CA), and straits or sounds (such as Ketchikan, AK), were generally not included. Additional criteria for station selection were a long, continuous data record, a constant tidal reference datum, and an even distribution of stations with distance along the coast. The stations selected and their locations are shown in Figure 5.1.

The processes affecting sea level are complex. In addition to the well-understood tidal or astronomic forces, sea level is affected by:

1. Changes in the average density of the water column.
2. Changes in distribution of atmospheric pressure over the ocean surface (resulting, in part, in variations in large scale wind patterns).
3. Variations in speed of alongshore components of ocean currents.
4. Changes in total mass of ocean water resulting from accretion or melting of glaciers.
5. Subsidence or emergence of the land upon which the gage is located.

The relative importance of these processes varies from station to station.

For ocean monitoring in support of fisheries assessment, we are interested in fluctuations with periods of months to years. For this reason the data are presented in terms of monthly means which remove the principal diurnal and semidiurnal periodicities from the data. Fluctuations with periods longer than months or years can be reduced by comparing the data with a 19-yr mean. This compensates for the nodal tide, which results from the changing declination of the moon over a period of 18.61 years. The nodal tide has a much greater "potential," or effect, than do

³Permanent Service for Mean Sea Level, Berkenhead, U.K., and National Ocean Survey, NOAA, Washington, DC 20852.

other long-period, astronomically induced, harmonics observed in tidal data (Lisitzin 1974). We did not, however, remove very long-period fluctuations such as those caused by isostatic glacial responses (as at Yakutat, AK) or fluctuations related to land subsidence or uplift (such as at Balboa, CZ).

Our objective is to compare temporal fluctuations of sea level along much of the eastern Pacific coast for eventual comparison with fishery fluctuations. In order to allow comparison between stations and to flag unusual events, the data are presented as monthly mean anomalies or departures of a given month from its long-term mean. The long-term means used in this report were for the 19-yr period, 1949-67. The tidal reference datum differs from station to station. Computation of anomalies at each station allows comparison in time between stations having different datum levels.

Pattullo et al. (1955) found that in temperate and tropic latitudes (between about 40N and 40S) changes in the specific volume of the water column were responsible for most of the nontidal variation in recorded sea level. Atmospheric pressure effects were found to account for only a small part of the recorded changes in sea level. This situation is not true, however, in higher latitudes. Lisitzin and Pattullo (1961) found that north of 40N much of the variation in sea level results from changes in distribution of atmospheric pressure over the ocean. This "inverted barometer" effect can be removed from the data in high latitudes by adjusting sea levels for departures of atmospheric pressure from a long-term mean.

There is evidence that fluctuations in atmospheric pressure are quickly followed by compensating changes in sea level so that the total pressure on the sea floor remains very nearly constant. This isostatic adjustment is thought to occur over a range of several thousand miles and within a time span of several days. Thus, the ocean can be considered to approach isostatic equilibrium with atmospheric pressure for periods of a month or more. Assuming the average pressure over the oceans remains constant, if the pressure difference between two stations changes, the sea surface slope will change to compensate for this difference so that there will be no net change in the distribution of pressure on the sea floor (Pattullo et al. 1955; Saur 1972).

Pressure effects were removed from the data by correcting sea levels to a long-term mean atmospheric pressure in the vicinity of the tide gage. This compensates for both the normal seasonal cycle and the monthly pressure anomaly. Monthly mean sea level pressure data were obtained from the World Weather Record series,

Monthly Climatic Data for the World, from CCEA,⁴ or computed from monthly mean pressure fields obtained from FNWC.⁵

Normal atmospheric pressures at each station were obtained by averaging monthly pressures for the entire period of record. The effects of monthly variations from this long-term pressure mean were removed from sea level measurements by applying a correction of 1 cm in sea level for each millibar deviation in atmospheric pressure. Sea level data for all stations north of Mazatlan were corrected in this manner, with resultant small decreases in the range of sea level anomalies. Pressure deviations south of Mazatlan were on the order of one millibar or less, not large enough to warrant correction because sea level measurements have a typical error of about 1 cm.

DISCUSSION

The anomalies of corrected monthly mean sea level (Figs. 5.2-5.6) exhibit remarkably coherent patterns in time and space. Perhaps the most striking feature of the time series is the long-term persistence and wide distribution of high sea level during the period 1957-59. Evidence of anomalously high sea level extends from Caldera, Chile, to Adak, AK. Similar periods of anomalously high sea level can be seen in 1940-41 and 1971-73, and to a lesser extent in 1951-52 and 1965-66.

The simultaneous occurrence of these changes over such vast distances suggests a relation to large-scale oceanic or atmospheric disturbances. The periods of anomalously high sea levels were also periods of anomalously warm sea surface temperatures and are associated with El Nino occurrences in the eastern tropical Pacific (Quinn 1976, 1978).

Such environmental changes can have dramatic effects on marine fisheries. Along the coast of Peru, for example, large changes in the distribution and abundance of anchoveta result from adverse oceanographic conditions associated with El Nino periods. These conditions, combined with heavy exploitation, have resulted in a decline of the fishery and have had major economic impact. Radpovich (1961) documented many changes in the distribution of marine populations along the coast of California during the warm water periods 1940-41 and 1957-59 which were associated with high sea levels. He found a general northerly shift of southern

⁴Center for Climatic and Environmental Assessment, Environmental Data Service, NOAA, Columbia, MO 65201.

⁵Fleet Numerical Weather Central, U.S. Navy, Monterey, CA 93940.

species and an increase in yellowtail and bonito populations off California. Changes of sea level related to fluctuating coastal circulation may be associated with variations in year class strengths of marine populations due to changes in larval transport.

In his investigation of low frequency sea level oscillations, Roden (1966) found a high coherence in sea level fluctuations measured by tide gages located within similar macroenvironments, such as those located within the Gulf of Alaska or within the California Current area. Even stations with dissimilar exposure, such as those with gages located on the open coast compared to those with gages located in enclosed bays, yielded similar results if the stations were within the same macroenvironment. We now examine fluctuations of sea level in groups of stations having similar oceanographic environments.

Aleutian Islands

Sea levels in this area are quite variable. Significant long-term lower sea levels can be seen at Adak (1943-51) and Attu (1952-53). In contrast to the low sea levels observed at Adak and Attu in 1952-53, Unalaska, Kodiak, and Yakutat show anomalously high values, with a peak in early 1953. There seems to be little correlation between Attu and neighboring stations. This suggests that sea level at Attu, which is located in an area of relatively free exchange between the Pacific Ocean and Bering Sea, may respond to a different combination of environmental processes than sea level at Adak, Unalaska, or Kodiak. It is interesting to note that Attu is the only station of the 25 examined that did not show anomalously high sea levels in 1957-59. Unalaska had small anomalies through 1956 and strong positive anomalies during 1957-59. In contrast, the periods 1964-67 and 1971-74 exhibit strong negative anomalies. This suggests long-term fluctuations in the ocean environment near Unalaska.

Gulf of Alaska - Pacific Northwest

Kodiak has the shortest record of observations in the series. It was included to fill a gap between widespread stations. It shows surprisingly small variations in sea level with extremes in 1957-58 and 1961-62. A weak positive anomaly with a peak in early 1958 is evident.

The Yakutat gage, located in a harbor, is subject to salinity changes due to increased river runoff during summer months (Favorite 1974). The trend of decreasing sea level seen in the series for this station results from land uplift due to isostatic glacial rebound. Strong negative anomalies are evident during 1955-56, 1961-62, and 1971-72. Surprising small positive

anomalies are seen during 1958. Favorite (1974) has shown that annual mean sea level anomalies at Yakutat were well correlated with mean annual wind stress transport anomalies in the Gulf of Alaska during the period 1950-59.

Fairly persistent long-term sea level anomalies with short-term fluctuations can be seen at Sitka, Prince Rupert, Tofino, Neah Bay, and Crescent City. Sea level fluctuations are remarkably coherent among these stations, considering the 1800 km along the coast between Sitka and Crescent City. Major periods of high sea level are seen during 1940-41 and 1957-59. Low sea level periods include 1955-56, late 1961-early 1962, and 1964. A significant period of anomalously low sea level is evident at Prince Rupert between the years 1947 and 1951.

California Current

Sea level data from San Francisco, Avila Beach, Los Angeles, and La Jolla also exhibit similar fluctuations. Periods of high sea level are noticeable during 1941, 1951-52, 1957-59, and 1972-73 at all stations. Periods of high sea level during 1969 were observed at San Francisco and Avila. Periods of low sea level occurred at all stations during 1955 and early 1956 and during 1964. A strong trend of rising sea level in relation to land occurred at all stations in this group.

Mexico - Central America

Mazatlan, Manzanillo, Acapulco, Balboa, La Union, and Buenaventura show similar patterns of sea level fluctuations. Periods of high sea level correspond very well with El Nino conditions (Quinn 1976, 1978). All stations exhibit very high sea levels during 1941-42, 1957-59, and, to a lesser extent, 1965-66. Extremely high levels were noted during 1972-73. The anomaly at Manzanillo for December 1972 measured 28.8 cm, one of the largest in the entire series. Anomalously low sea levels were seen in 1949-50, 1955, and 1967. The station at Balboa shows a trend of rising sea level which Roden (1963) attributed to land subsidence.

Peru Current Region

Talara, Callao, Matarani, Antofagasta, and Caldera also show remarkably coherent fluctuations in sea level. Like the group of stations to the north, periods of high sea level correspond well with El Nino conditions. The 1941-42 period of high sea levels is evident at Matarani. The 1957-59 and 1965 periods of high sea levels are seen at all stations in this region. During 1972, a period of extremely high sea levels occurred at Talara peaking at 36.5 cm in December 1972. A maximum anomaly of 34.4 cm was measured at Talara during November 1974. It is interesting to

note the sharp spike of extremely low sea level that occurred just before the 1974 period of high sea level at Talara. Anomalously high sea levels are also evident at Callao during 1972. Periods of low sea level occurred at all stations in this group during 1949-50, 1954-56, and 1966-67.

CONCLUSION

Anomalies of monthly mean sea level observations along the west coast of North and South America persist for periods ranging from several months to two years or longer and are coherent in space for hundreds of kilometers. Anomalous "events" can be traced along the coast from Chile to Alaska and may be related to coastal circulation processes which may in turn affect larval drift and reproductive success of marine organisms. Certainly the major periods of anomalously high sea level during 1941-42, 1957-59, and 1972 were associated with unusual changes in the abundance or distribution of many marine species. It is hoped that further research on the factors affecting sea level will lead to a better understanding of ocean circulation processes and their effects on populations of marine organisms.

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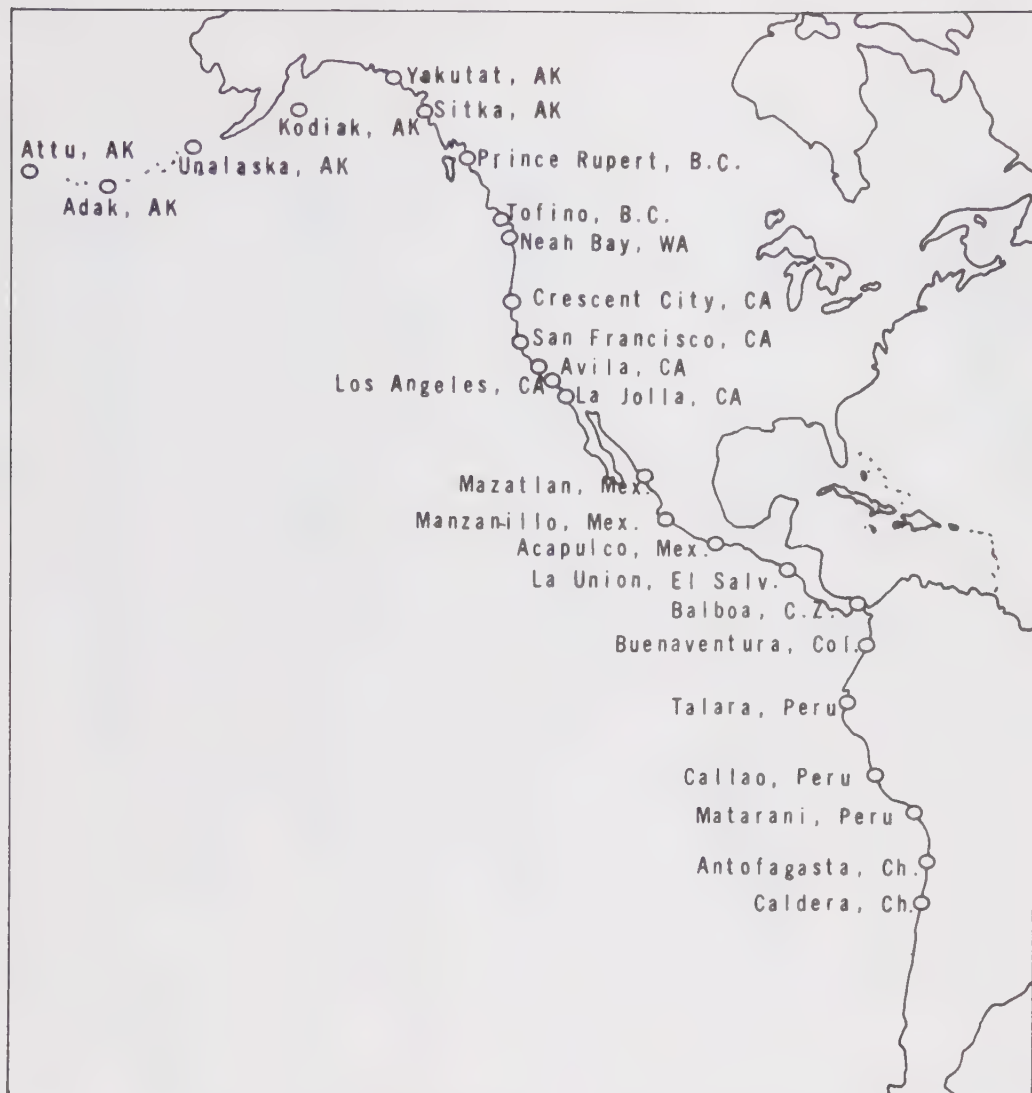


Figure 5.1.—Selected tide stations along the west coast of North and South America.

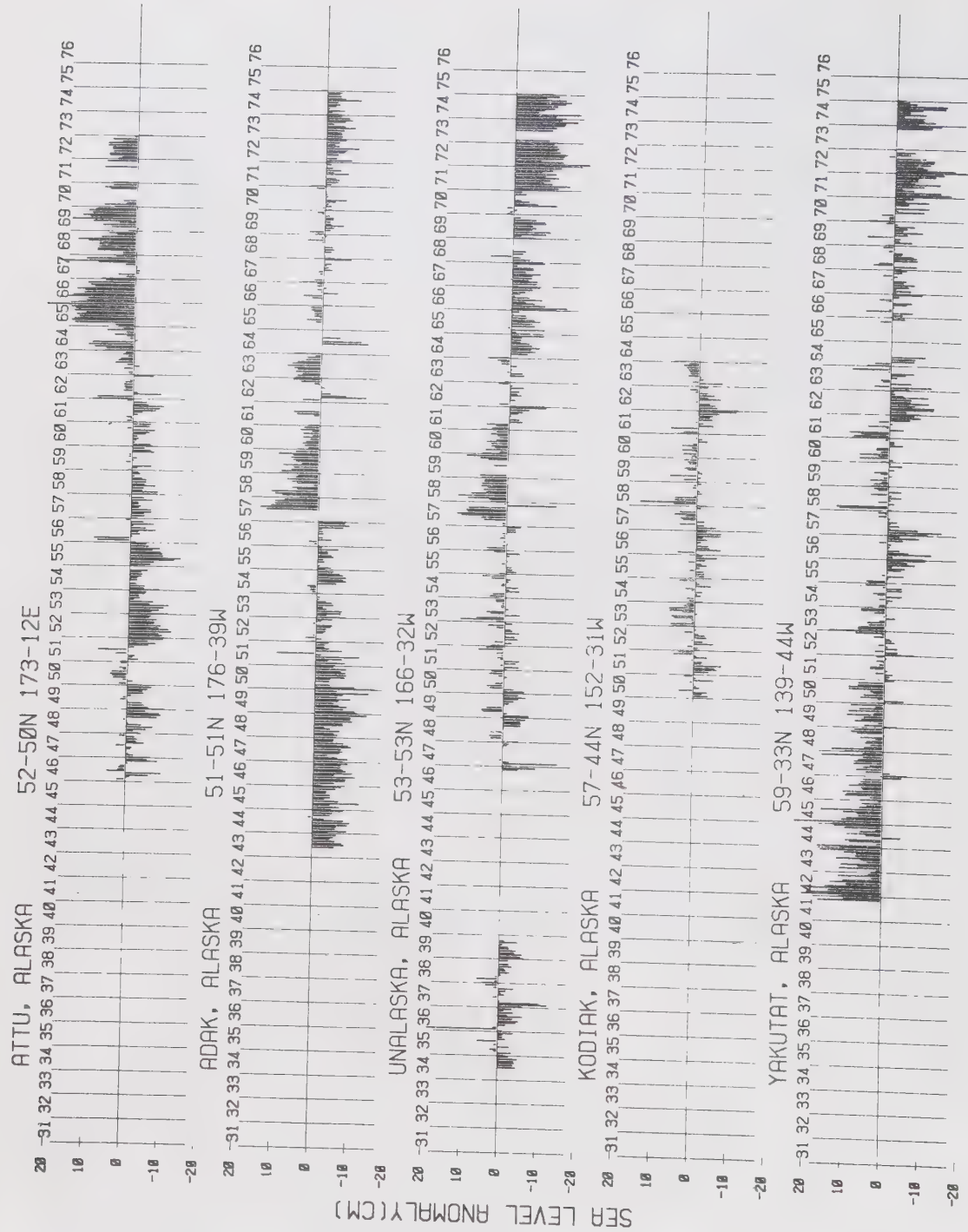


Figure 5.2.—Anomalies of mean sea level for stations in the Aleutian Islands and Gulf of Alaska.

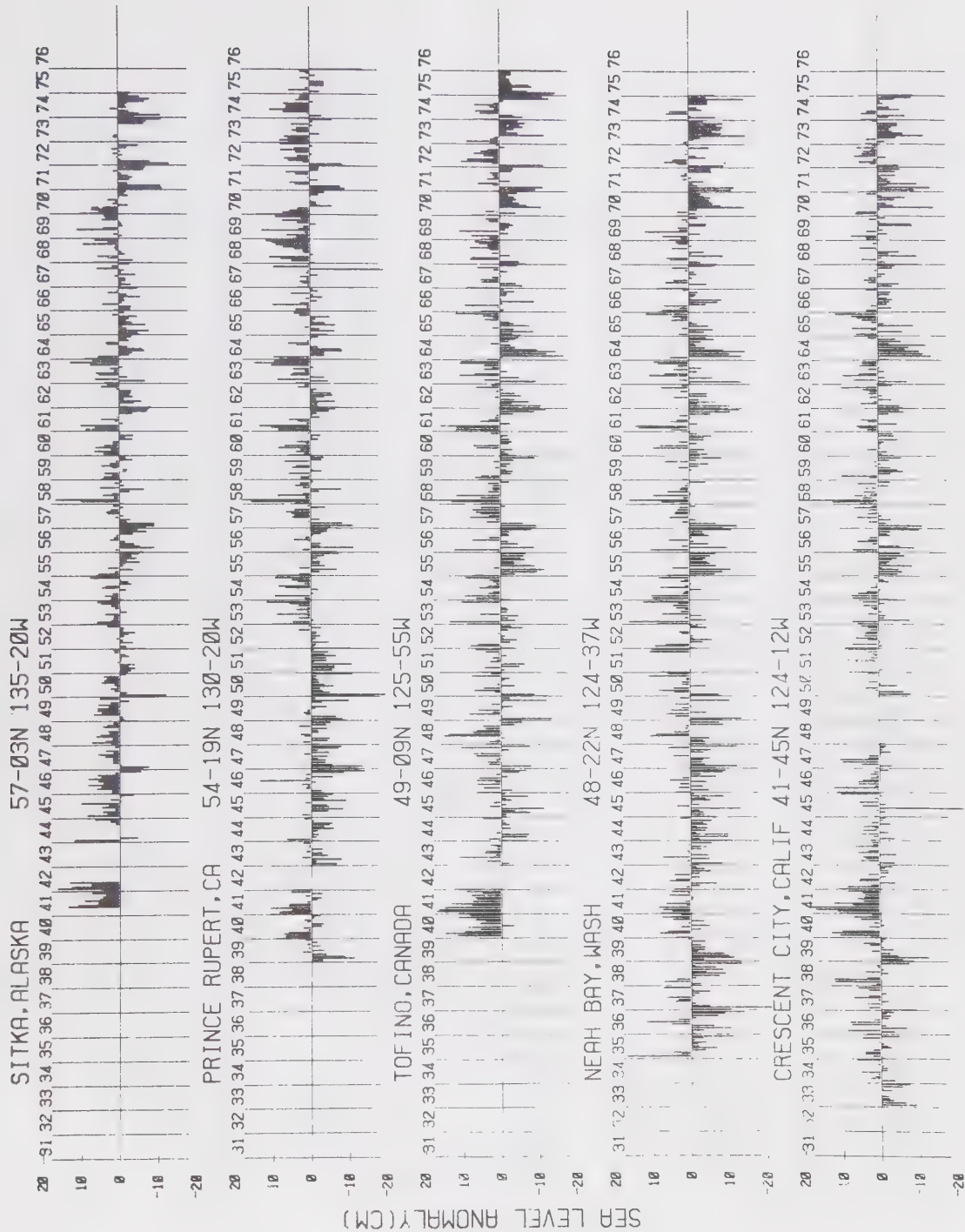


Figure 5.3.—Anomalies of mean sea level for stations in the Gulf of Alaska and Pacific Northwest.

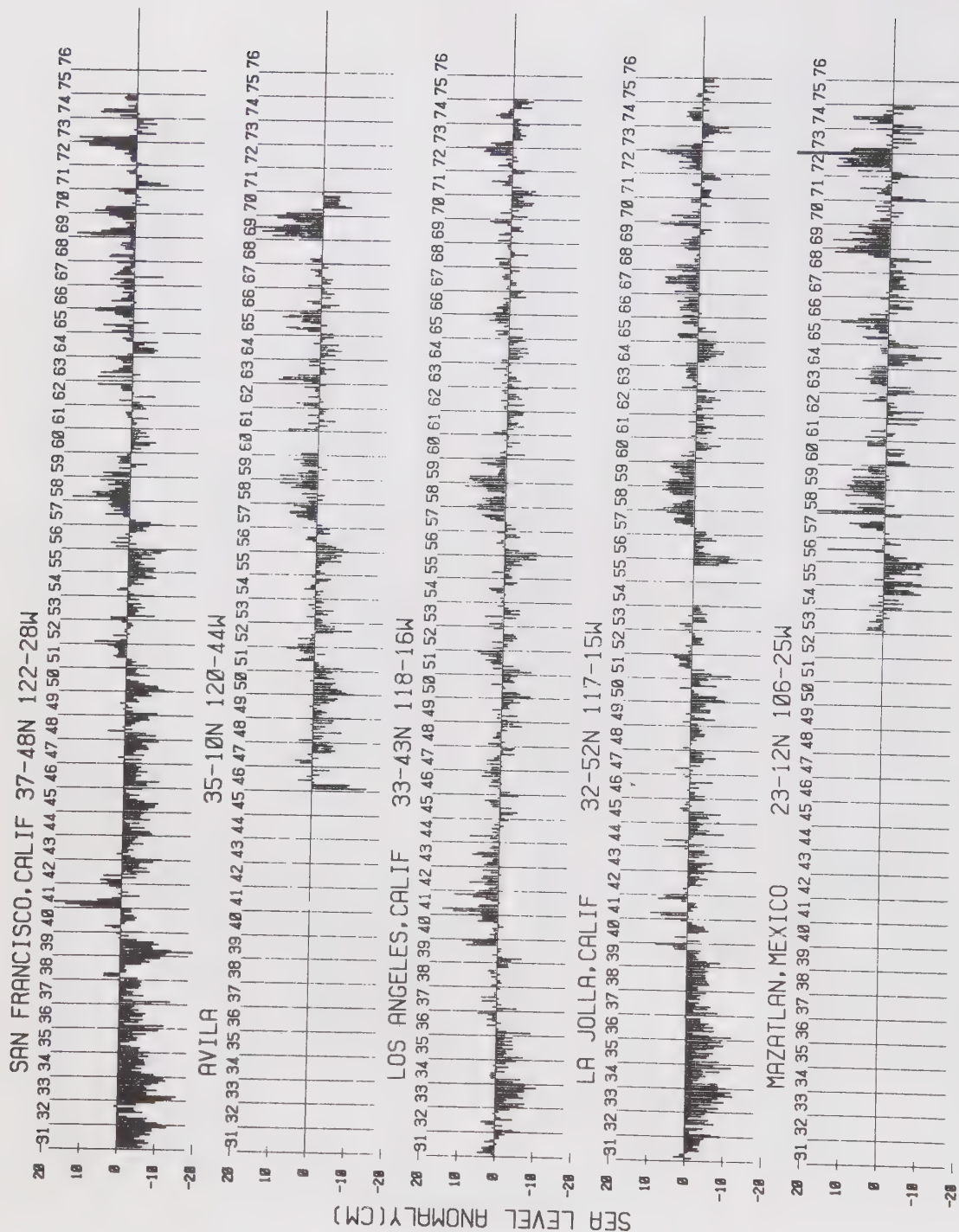


Figure 5.4.—Anomalies of mean sea level for stations in the California Current area and northern Mexico.

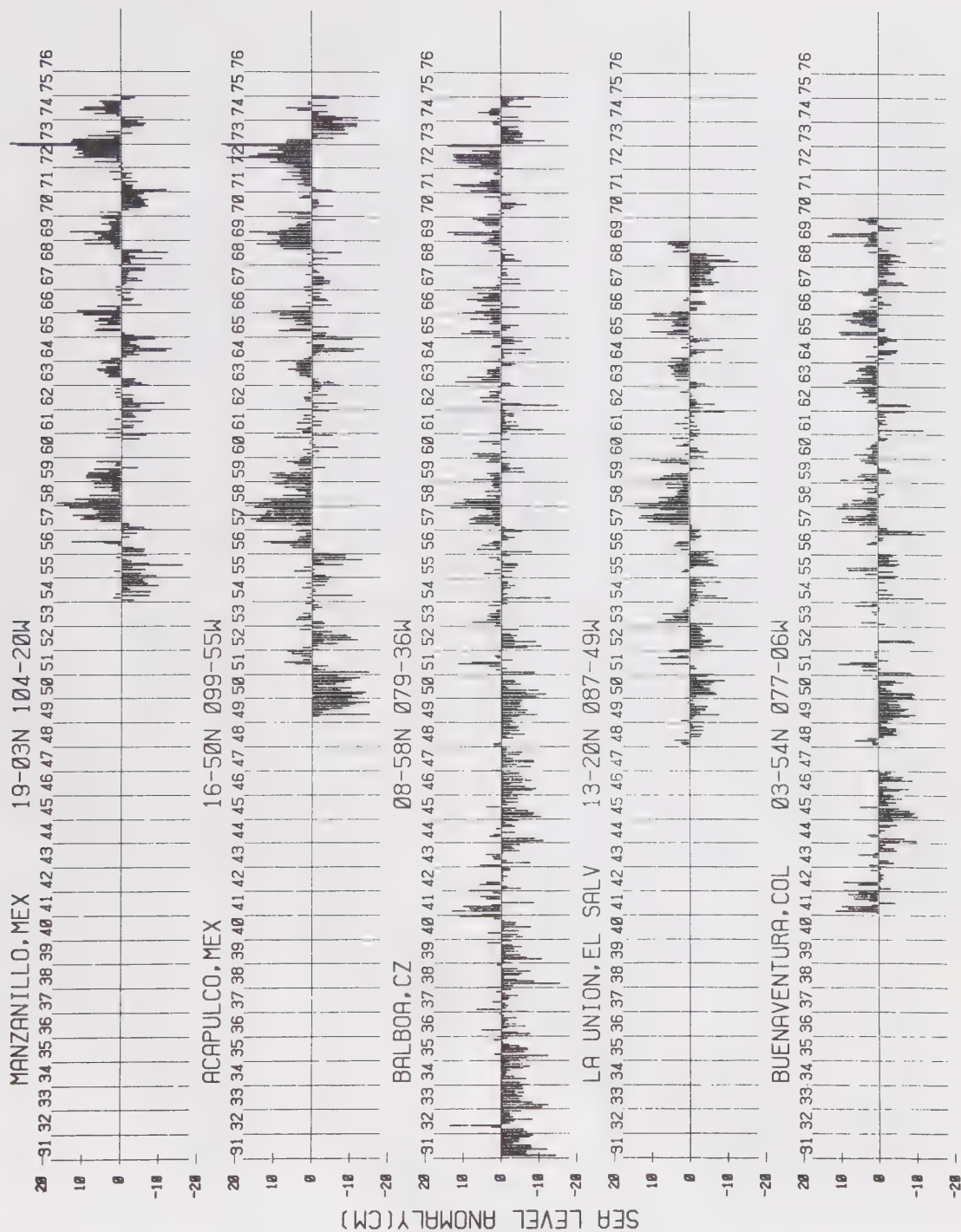


Figure 5.5.—Anomalies of mean sea level for stations in Mexico and Central America.

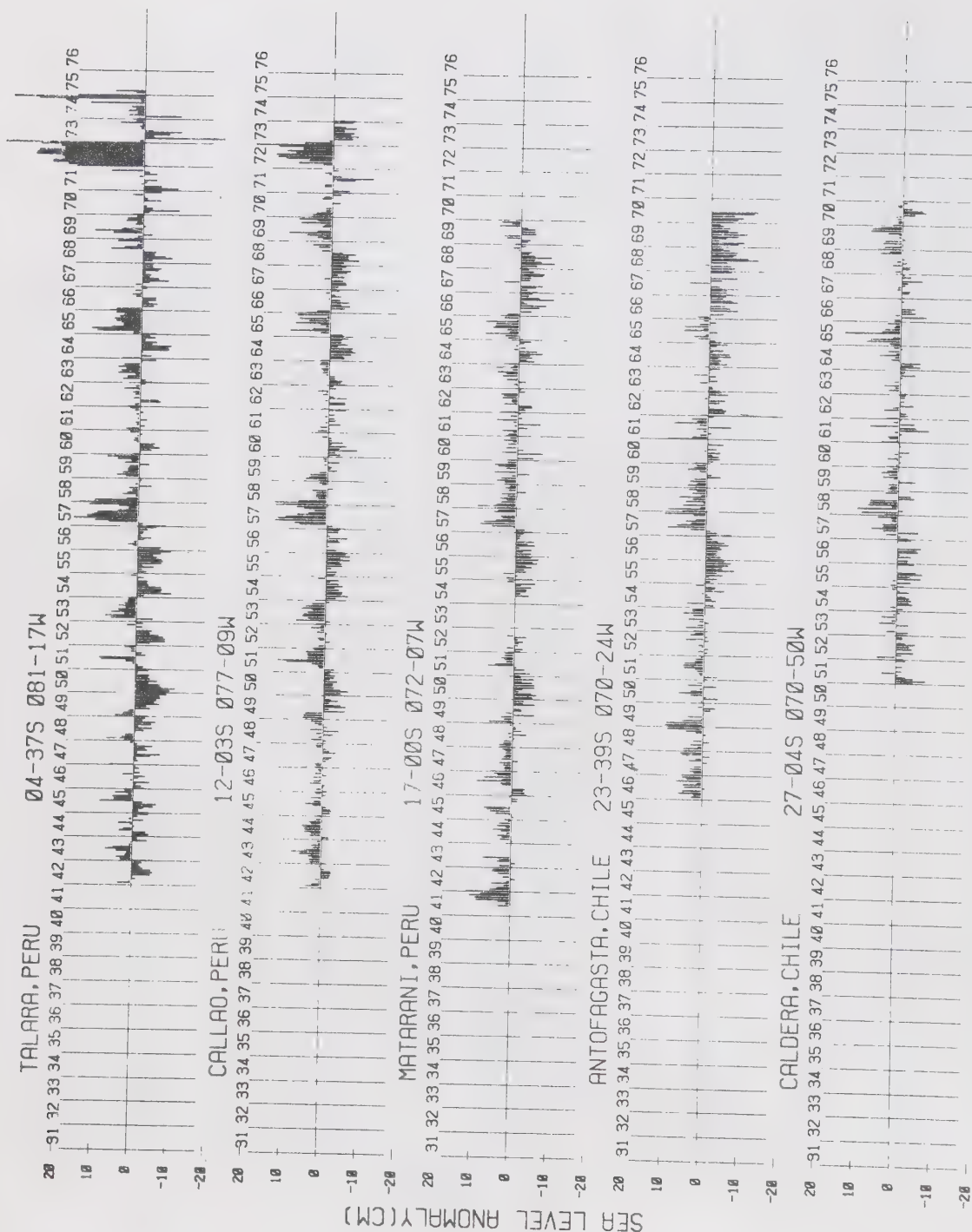


Figure 5.6.—Anomalies of mean sea level for stations in the Peru Current area.

THE EFFECT OF BODY SIZE ON
THE STANDARD METABOLIC RATE OF
SKIPJACK TUNA, *KATSUWONUS PELAMIS*

The standard metabolic rate (SMR) of fish is the energy requirement of a postabsorptive animal completely at rest (Beamish and Mookherjee 1964; Fry 1971; Brett 1972). It approximates the energy demand of all metabolic processes except swimming and digestion. The SMR (and its relation to fish size) is an important input parameter for energetics, growth, and population models (Kitchell et al. 1974; Kitchell et al. 1977). The SMR may also be used to predict optimal fish cruising speed (Weihs 1973, 1977). I undertook this study to provide SMR measurements for skipjack tuna, *Katsuwonus pelamis*. These measurements may be incorporated into models such as those described in Sharp and Francis (1976), Kitchell et al. (1978), and Sharp and Vlymen (1978).

The SMR is generally determined by extrapolation of a metabolic rate versus swimming activity curve back to a zero activity level (Beamish 1964; Brett 1965; Muir et al. 1965). However, because it is difficult simultaneously to measure metabolic rate and activity level of large, highly active, pelagic species such as skipjack tuna, SMR was measured directly.

Methods and Materials

Skipjack tuna, purchased from local fishermen, were maintained at the Kewalo Research Facility of the National Marine Fisheries Service (described in Nakamura 1972). Fish were kept in outdoor tanks from 2 days to several weeks before use. Food was presented to all fish daily; however, a fish was not fed for at least 20 h prior to its use in an experiment. This allowed sufficient time for an animal to clear its stomach and intestine and for its blood glucose level to return to prefeeding levels (Magnuson 1969).

To reduce struggling and minimize injury during handling, each fish was injected with the neuromuscular blocking agent gallamine triethiodide (approximately 1 mg kg^{-1}). The animal was then placed in a Plexiglas¹ flow-through box respirometer, similar to that described in Stevens (1972). The spinal cord was cut immediately behind the skull to stop all overt muscular activity

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

and the wound packed with foam rubber to minimize bleeding. Electrocardiogram (ECG) leads were mounted subcutaneously on the ventral body surface and an 18-gage hypodermic needle, with a thermistor bead mounted in its tip, was pushed through the dorsal musculature to the vertebral column. The ECG signal was displayed on an oscilloscope and the red muscle temperature determined by balancing a wheatstone bridge circuit containing the needle mounted thermistor and a 5-decade resistance substitution box.

Oxygen concentration of the water upstream and downstream of the fish was monitored simultaneously with two Yellow Springs Instruments (model 51A) dissolved oxygen meters equipped with Clark-type, polarographic electrode, oxygen-temperature probes. Water flow through the respirometer was maintained at approximately 3 l kg^{-1} (body weight) min^{-1} , and was measured by recording the time required to fill a 1 l graduated cylinder. The source of the seawater was the same as that which supplied the holding tanks. No at-

tempt was made to control water temperature which ranged from 23.5° to 25.5° C .

Dissolved oxygen levels, water flow rate, heart rate, red muscle temperature, and water temperature were determined every 10 min and measurements were continued until the fish's metabolic rate remained relatively stable for at least 1 h.

Results and Discussion

The SMR of each fish was determined by finding the minimum predicted metabolic rate based on a second degree polynomial fitted to observed metabolic rate measurements. This method is an acceptable approximation for asymptotic curve fitting (Snedecor and Cochran 1967). To illustrate this technique, the observed and predicted metabolic rate, body temperature, and heart rate are presented in Figure 1.

Heart rate was monitored only as a check on the health of the animal. Experiments were terminated if the heart rate became erratic or slowed

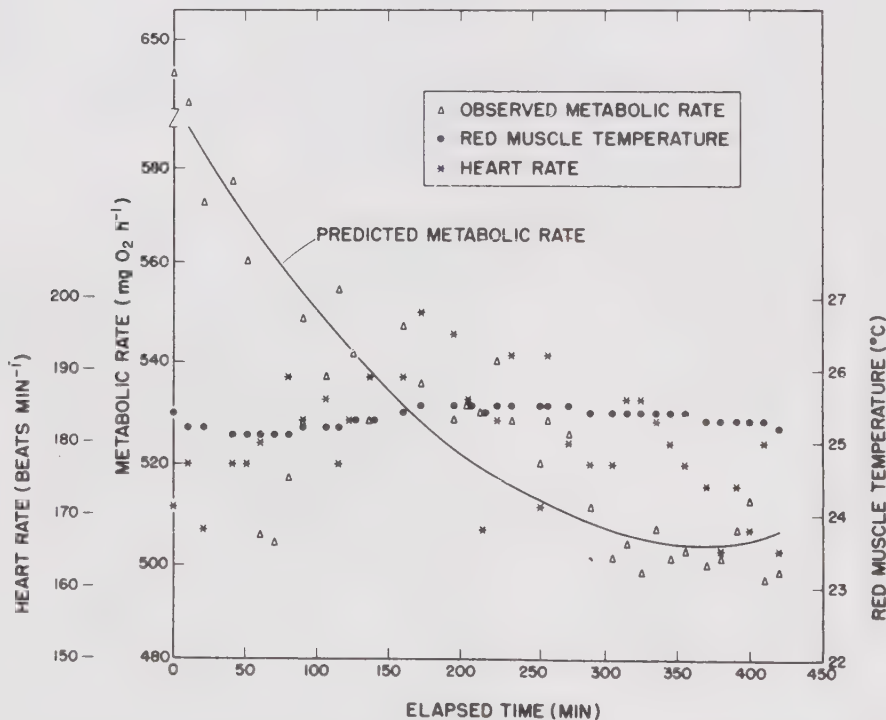


FIGURE 1.—Changes in metabolic rate, heart rate, and red muscle temperature of a 1.456 kg skipjack tuna during an experiment to determine standard metabolic rate (SMR). The predicted metabolic rate is based on a least-squares fitted second degree polynomial. The minimum predicted metabolic rate (i.e., SMR) is $505 \text{ mg O}_2 \text{ h}^{-1}$.

significantly. Red muscle temperature was monitored to test if changes in metabolic rate reflected changes in it. All fish showed red muscle temperatures as stable as those shown in Figure 1. Fish were in the respirometry box approximately 15 to 30 min before data recording began and red muscle temperatures generally approached thermal steady state during this period.

The SMR of 33 fish (0.317–4.737 kg) was successfully determined. A regression line of SMR versus body weight was fitted by Gauss-Newton iteration technique (Biomedical Computer Programs, program number BMDP 3R), rather than by a linear regression technique based on log-log transformation of the data (Figure 2). The advantages of the former method and disadvantages of the latter have been discussed by Zar (1968) and Glass (1969).

The best-fitting allometric equation was found to be:

$$\text{SMR} = 412.0 (\pm 27.1) W^{0.563 (\pm 0.07)} \quad (1)^2$$

where SMR = standard metabolic rate in milligrams O_2 per hour and
W = body weight in kilograms;

values in parentheses are the standard deviations of the parameters. The coefficient of determination (r^2) is 0.72.

The exponent in the allometric equation describing the effect of body size on the SMR of other teleosts ranges from approximately 0.65 to >1 (Winberg 1956; Fry 1957; Beamish and Mookherjee 1964; Beamish 1964; Glass 1969; Brett 1972). The lower value for the exponent in Equation (1) indicates that the weight specific SMR (i.e., milligrams O_2 per gram per hour) of skipjack tuna decreases more steeply as body size increases than does the weight specific SMR of other species.

The strong influence of body size on the SMR may be a unique characteristic of thermoconserving species such as skipjack tuna. However, the value of the weight exponent could also be influenced by the technique used to measure SMR. For comparative purposes, it would be useful to determine the SMR's (and corresponding allometric equation) of species (e.g., salmonids) where

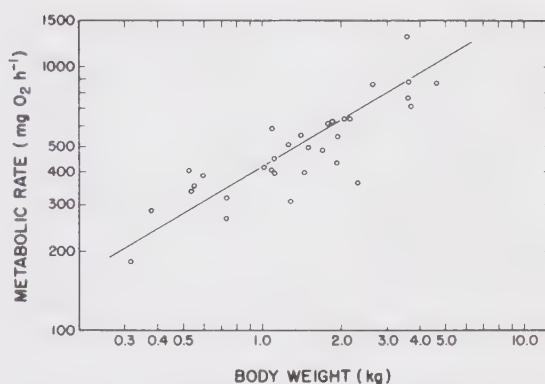


FIGURE 2.—A double logarithmic plot of the standard metabolic rate (SMR) versus body weight (W). The line represents the allometric equation $\text{SMR} = 412.0 W^{0.563}$. The coefficient of determination is 0.72.

these parameters are already known, but employing the methodology outlined in this study.

The SMR has been postulated to be a function of: the diffusing capacity of the respiratory system, whole blood sugar concentration, and the rate at which the circulatory system can deliver substrates and oxygen to the cells (Schmidt-Nielsen 1970; Ultsch 1973; Coulson et al. 1977; Wilkie 1977; Hughes 1977; Umminger 1977). Specifically which of these factors most influence the SMR of skipjack tuna is unknown at this time. Selection pressures apparently favor significant reductions in the weight-specific SMR of skipjack tuna as body size increases (hence the lower exponent in Equation (1)). How the factors that determine SMR could be affected by such selection pressures is also unknown.

The SMR's for skipjack tuna are approximately 5 to 10 times greater than those reported for other teleosts of equal body size (Pritchard et al. 1958; Beamish 1964; Brett 1965, 1972). However, the great difference in the effect of weight on SMR, and the unique methodology employed in this study, makes direct comparisons tenuous.

Application of the Results

Careful application of my results in energetics models is advised for several reasons. First, skipjack tuna attain maximum body size of approximately 22 kg (Kitchell et al. 1978); although the weight range of fish I used in this study covers more than an order of magnitude, there is still a large untested size range. Because skipjack tuna

²If the allometric equation to describe the effect of body size on whole body SMR is: $\text{SMR} = aW^b$ then the corresponding equation to describe weight-specific SMR versus body weight is: $\text{SMR}/W = aW^{b-1}$ or $\text{SMR}' = aW^{b-1}$ where SMR' = weight-specific SMR, W = body weight, and a and b are fitted parameters.

>4 to 5 kg are extremely difficult to capture and transport, it is unlikely that specimens larger than this will be tested in the foreseeable future.

Second, the SMR includes the energetic cost of osmoregulation and cardiac work. The energy requirement of both processes comprises a significant fraction of the SMR (Heath 1964) and more importantly, the energy demand of these processes is dependent on swimming speed (Rao 1968; Farmer and Beamish 1969; Nordlie and Leffler 1975). Therefore prediction of energy demand as a function of swimming speed may not be adequately determined by simple addition of the SMR and the energy cost of swimming based on a theoretical estimate of hydrodynamic drag; an estimate of the increased internal work, due to activity, should also be included.

Third, the scatter in the SMR's presented in Figure 2 is due, in part, to the difficulty of working with animals such as skipjack tuna, which are both highly active and physiologically delicate. There are, however, also at least two distinct subpopulations of skipjack tuna that occur around the Hawaiian Islands (Sharp³). It is reasonable to suspect the SMR of individuals from the various subpopulations might be significantly different when measured under identical conditions. Again, reasonable caution in application of the data presented here is urged.

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Effect of temperature on isotonic twitch of white muscle and predicted maximum swimming speeds of skipjack tuna, *Katsuwonus pelamis*

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Keywords:

White muscle, contraction time, swimming speed, skipjack tuna, *Katsuwonus pelamis*

Synopsis

Latent period, rise time, contraction time, and half relaxation time from isotonic contractions of isolated white muscle samples from skipjack tuna, *Katsuwonus pelamis*, were determined at 20°, 27°, and 34° C. These parameters were found to be inversely proportional to temperature ($Q_{10} = 1.47, 1.67, 1.62, \text{ and } 1.72$, respectively). The data show that contraction time and the effect of temperature on contraction time of skipjack tuna white muscle are not unique when compared to other equal-sized teleosts. Based on contraction time, maximum swimming speeds at each muscle temperature were calculated and found not significantly to exceed the maximum speeds of other equal-sized teleosts, when comparisons are made at the same white muscle temperatures.

Introduction

Descriptions of the specialized vascular anatomy (the countercurrent heat exchangers or so-called 'rete mirabile') of tuna have been available for over 50 years (Kishinouye 1923). In spite of numerous measurements of muscle temperatures and thermal profiles (reviewed in Stevens & Neill 1978), the biological significance of tuna's specialized vascular anatomy and resultant elevated muscle temperatures has not yet been empirically defined nor quantified.

Temperature has multiple effects on muscle contraction. Higher temperature causes a higher rate of T

tubule inward transmission, increased rate and possibly amount of Ca^{+2} release from the terminal cisternae, faster Ca^{+2} diffusion to the actin and myosin overlap zone (A band), and increased rate of Ca^{+2} uptake by the sarcoplasmic reticulum. The higher levels of Ca^{+2} cause more actin sites to become available for combination with myosin (i.e., more actin-myosin cross bridges), and higher rates of cross bridge cycling (reviewed by Fuchs 1974). Therefore, the overall effects of higher muscle temperature are shorter latent period, increased speed of contraction at a given load, increased intensity of active state, decreased duration of the active state plateau, and faster tension decay (Truong et al. 1964, Close & Hoh 1968, Gabel et al. 1968, Podolsky 1968).

Power is defined as force times velocity. Higher muscle temperatures cause increased speed of contraction, hence (assuming force stays constant with increasing speed), increased power output per contraction (Binkhorst et al. 1977). Higher muscle temperatures also permit higher frequencies of contraction, and hence, increased average power output during repeated contractions (such as swimming).

It is, therefore, reasonable to conclude that tuna evolved their specialized circulatory system and elevated muscle temperatures to increase muscle power output (as suggested by Carey et al. 1971). Carey (1973) and Graham (1975) have specifically argued that the elevated muscle temperatures and external morphological adaptations of tuna evolved to increase maximum swimming speeds (see also Walters 1962) and that tuna are capable of exceptional maximum speeds. Yet Walters & Fierstine

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(1964) have shown that the maximum speed of wahoo, *Acanthocybium solandri*, is nearly identical to the maximum speed of equal-sized yellowfin tuna, *Thunnus albacares*, even though the former species does not have the specialized circulatory system required to maintain muscle temperature significantly above ambient temperature (Collette 1978). Furthermore, Blaxter & Dickson (1959) and Brett (1964) reported that the measured maximum swimming speeds of several teleost species are temperature independent. However, their data are hard to reconcile with evidence that the average power available from isolated teleost muscle samples (and, therefore, predicted maximum swimming speed) is indeed inversely proportional to temperature (Wardle 1975, 1977).

For the following reasons, we feel it is an open question whether tuna are unique with respect to their maximum swimming speeds, and whether their specialized vascular anatomy evolved to permit higher maximum speeds. First, widely different techniques have been employed to measure the maximum swimming speeds of different species (Blaxter 1969). Second, fish size and water temperature are often either not reported, or not known with certainty. Third, the definition of maximum (or burst) speed is not consistent throughout the literature. Bainbridge (1958) defines burst speed as the highest swimming speed maintained for at least one minute. But the maximum speeds of yellowfin tuna and wahoo, given by Walters & Fierstine (1964) were maintained for less than one second. Moreover, the measurements of tuna's burst speeds were taken in water at 24–27° C. The maximum swimming speeds of other teleosts are generally measured in water 10–20° C (Blaxter 1969).

Our study was undertaken to determine the effect of temperature on several parameters of the isotonic twitch of white muscle samples from skipjack tuna, *Katsuwonus pelamis*. Using a technique presented by Wardle (1975), we use our results to predict maximum swimming speeds at various muscle temperatures, and in this way, quantify the relationship between muscle temperature and predicted maximum swimming speed.

Materials and methods

Skipjack tuna, purchased from local fishermen, were maintained at the Kewalo Research Facility of the National Marine Fisheries Service. Nakamura (1972) provides details on capture and handling.

Five fish were used; each was removed from its holding tank, brought into the laboratory, and placed in a plexiglass trough lined with foam rubber. A hose with running seawater (24° C) was inserted into the fish's mouth. The spinal cord was cut immediately behind the skull, and the wound packed with Gel-Foam (Upjohn Pharmaceuticals)³ to minimize bleeding. The animal was then rested for 1 hour before muscle samples were removed.

Samples consisted of muscle blocks approximately 2 × 1 × 1 cm. (The long axis of the block corresponded to the anterior-posterior axis of the fish.) The muscle blocks were impaled on two stainless steel stimulating electrodes mounted on a micromanipulator. The stationary electrode was fashioned from the barrel of a 15-gage hypodermic needle, the second (movable) electrode was a solid stainless steel needle (0.1 mm maximum diameter). The distance between the electrodes was slightly adjusted as required to fit the length of the muscle blocks. Both electrodes were insulated to the tip. Square wave, direct current pulses (10–100 V, 1 ms duration) were used to stimulate the muscle.

The movable electrode was connected by a short length of nylon thread to an isotonic, photoelectric force transducer (Myograph A, # 705–001, Narco Biosystems, Houston, TX). Transducer output was displayed on a storage oscilloscope and photographed with a 35 mm camera. The photographs were analyzed on a microfilm reader.

During testing, muscle blocks were immersed in a temperature regulated bath containing tuna muscle Ringer's solution.⁴ Test temperatures were 20°, 27°, and 34° C (± 0.2° C), which approximately span skipjack tuna's thermal habitat (Blackburn 1965). To change temperature, the bath was drained and refilled with fresh Ringer's solution at the appropriate

³ Reference to trade names does not imply endorsement of the product by the National Marine Fisheries Service, NOAA.

⁴ The Ringer's solution used in this study was based on Saither and Rogers (1967) and Hudson (1968). Ion concentrations approximate tuna plasma.

Salt	Weight (g)
NaCl	10.85
KCl	0.382
CaCl ₂ · 2H ₂ O	0.556
MgCl ₂ · 6H ₂ O	0.226
NaHCO ₃	1.26
NaH ₂ PO ₄ · H ₂ O	0.413
Glucose	1.00
Distilled H ₂ O to 1 liter	

temperature. The muscle block was left for 2–3 minutes at the new temperature before testing was resumed. Temperature sequence was randomized. Five to seven twitches were recorded at each temperature, and muscle blocks were discarded after being tested at all three temperatures. No more than 10 muscle samples were taken from any one fish.

Results

Effect of temperature on the isotonic twitch

Four measurements were taken from each oscilloscope tracing of a single twitch: (1) the time from stimulation to the maximum height of contraction (contraction time); (2) the time from stimulation to the onset of contraction (latent period); (3) the time from the onset of contraction to maximum height of contraction (rise time) (note, contraction time = latent period + rise time); and (4) the time from maximum height of contraction to one-half maxi-

mum height of contraction (half relaxation time).

Increased temperature caused reduced contraction times because of a significant reduction in both latent period and rise time (Fig. 1). The causes of the significant interfish differences in contraction time, within each test temperature, are not known. These differences are not, as might be expected, due to fish size (Hill 1956). The skipjack tuna used in this study ranged from only 36.6 to 42.9 cm fork length and are numbered in order of decreasing size (Table 1).

Figure 2 shows that half relaxation time is also inversely proportional to temperature.

The Q_{10} values, based on measurements made at 20° and 34° C are listed in Table 1. Apparently temperature has a smaller effect on latent period than on the other parameters. The Q_{10} for contraction time (and, therefore, predicted maximum swimming speed) was 1.62.

Predicted maximum swimming speeds

Contraction time is used to predict maximum swimming speed based on the following assumptions: (1) white muscle is used for high speed swimming (Bone 1975); (2) tail beat amplitude is independent of swimming speed; skipjack tuna, therefore, move a constant fraction of their body length per tail beat cycle (Bainbridge 1958, Hunter & Zwiefel 1971,

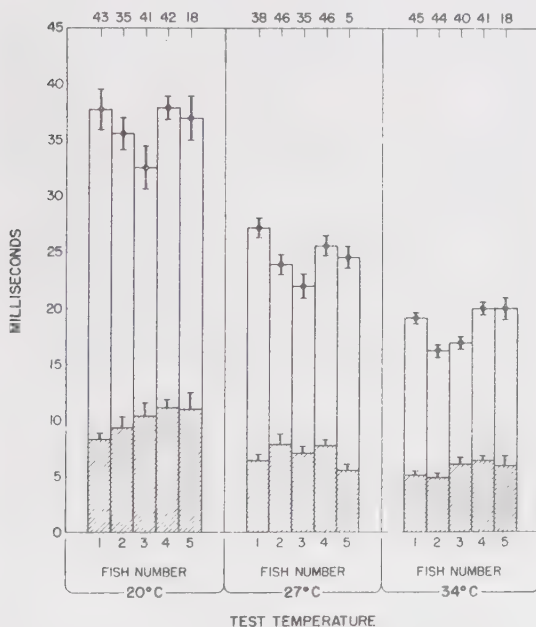


Fig. 1. Mean contraction times and mean latent periods (shaded area) at each test temperature. Vertical lines indicate 95% confidence limits, and numbers above each bar are total number of twitches used to determine each mean. (The film record for fish no. 5 was damaged during processing.)

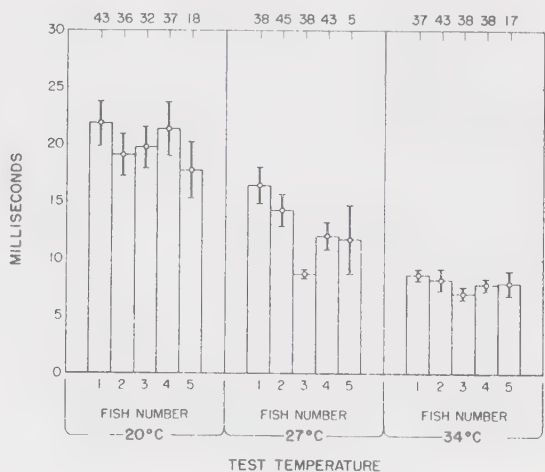


Fig. 2. Mean half relaxation times at each test temperature. Vertical lines indicate 95% confidence limits, and numbers above each bar are total number of twitches used to determine each mean.

Hudson 1973, Brill & Dizon MS⁵) at all swimming speeds; (3) maximum swimming speed is limited by maximum tail beat frequency (Wardle 1975); and (4) tail beat frequency is limited by the isotonic contraction times of two sets of laterally opposed muscles (Wardle 1975).

Maximum swimming speed ($U_{\max}$ in body lengths per second) is therefore predicted by:

$$U_{\max} = A / (2 \cdot C_t) \quad (1)$$

where A is the stride length coefficient (i.e., the fraction of fork length traveled per complete tail beat cycle) and C_t is contraction time, in seconds.

Also, maximum tail beat frequency (F_t) is predicted by:

$$F_t = 1 / (2 \cdot C_t) \quad (2)$$

By substituting maximum tail beat frequency into an empirically determined regression equation relating swimming speed to tail beat frequency in skipjack tuna (Yuen 1966), we were able to arrive at a second estimate for maximum swimming speed. Figure 3 gives predicted maximum speeds at each test temperature based both on a stride length coefficient of 0.7 (Bainbridge 1978, Brill & Dizon MS, see footnote 5) and the Yuen (1966) regression equation.

Table 1. Fork lengths, weights, and Q_{10} relationships.

Fish No.	Fork length (cm)	Weight (g)	Q_{10} ^a			
			Latent period	Rise time	Contraction time	Half relaxation time
1	42.9	1,040	1.41	1.69	1.62	1.72
2	40.6	749	1.57	1.83	1.75	1.64
3	39.9	752	1.46	1.71	1.60	1.84
4	39.1	713	1.48	1.63	1.58	1.80
5	36.3	778	1.55	1.50	1.55	1.60
Mean			1.49	1.67	1.62	1.72
Standard deviation			0.07	0.12	0.08	0.10

a. The Q_{10} values were calculated as follows:

$$Q_{10} = \left(\frac{P_{20^\circ}}{P_{34^\circ}} \right)^{10^\circ / 34^\circ - 20^\circ} \quad \text{where: } P_{20^\circ} = \text{latent period, rise time, contraction time or half relaxation time measured at } 20^\circ \text{ C, in msec, } P_{34^\circ} = \text{latent period, rise time, contraction time, or half relaxation time measured at } 34^\circ \text{ C, in msec.}$$

time, contraction time or half relaxation time measured at 20° C, in msec, P_{34° = latent period, rise time, contraction time, or half relaxation time measured at 34° C, in msec.

⁵ Brill, R. W. & A. E. Dizon. Red and white muscle fiber activity in swimming skipjack tuna, *Katsuwonus pelamis* (Linnaeus). Manuscript in preparation.

Discussion

We chose the standard parameters of latent period, rise time, contraction time, and half relaxation time to characterize the effect of temperature on our isolated muscle samples, rather than maximum twitch tension (force), for the following reason: The maximum force developed during a twitch is a function of both the intensity and duration of active state (Gabel et al. 1968). Because the physiological processes affecting these two parameters may have widely different Q_{10} relationships, the effect of temperature on maximum twitch tension is a complex phenomenon. Maximum twitch tension is, therefore, not a uniquely suitable measure to characterize the influence of temperature on muscle contraction (Hill 1951, Truong et al. 1964). Furthermore, we chose to use an isotonic (rather than an isometric) system to make our results directly comparable to the data presented by Wardle (1975, 1977).

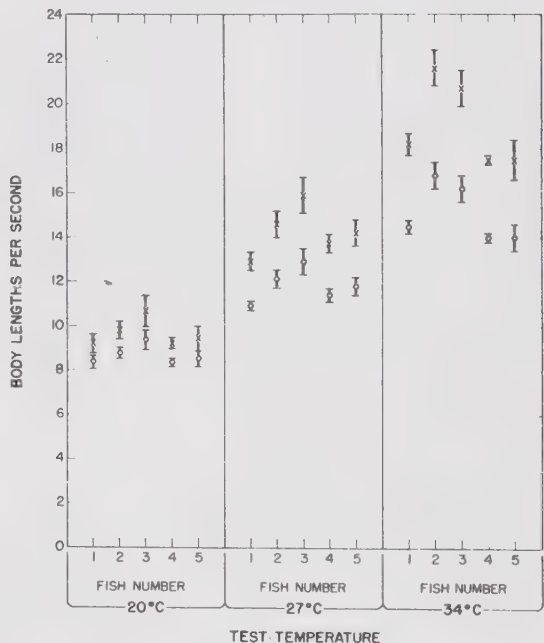


Fig. 3. Predicted maximum swimming speeds versus muscle temperatures. Open circles (o) represent maximum swimming speeds based on tail beat frequency versus swimming speed regression equation presented by Yuen (1966); crosses (x) are based on a stride length coefficient of 0.7. Vertical bars are based on 95% confidence intervals of contraction times.

Comparing Figure 1 with the data presented in Wardle (1977) indicates that, at 20° C, contraction times of muscle samples from skipjack tuna are equal to or longer than the contraction time of muscle samples from other teleosts of equal fork length. As for the effect of temperature, Q_{10} values were calculated based on measurements taken at 20° and 34° C, so as to estimate the effect of temperature over the approximate operating temperature range of skipjack tuna white muscle (Stevens & Neill 1978). The Q_{10} for contraction time of skipjack tuna white muscle ($Q_{10} = 1.67$) is only slightly higher than that for other teleosts ($Q_{10} = 1.4$, Wardle 1977, estimated from measurements taken at 14° and 20° C).

Therefore, in spite of other adaptations for high speed swimming (Fierstine & Walters 1967, Magnuson 1978), skipjack tuna white muscle appears not to be physiologically unique, in comparison with other teleosts, with respect to contraction time, or the effect of temperature on contraction time.

There are apparently no data in the literature concerning the effect of temperature on latent period, rise time or half relaxation time in fish muscle. Therefore, no comparisons can be made.

Accuracy of predicted maximum swimming speeds

Owing to the complex orientation of teleost myomeres (Fierstine & Walters 1967, Alexander 1969), it is almost impossible to isolate muscle samples with parallel fibers. Absolute values for maximum force development or maximum speed of contraction cannot be measured. However, contraction time (the parameter of interest with respect to predicting maximum swimming speed) is supposedly independent of after load, muscle sample size, and fiber orientation (Wardle 1975).

The 0.7 stride length coefficient (Bainbridge 1958) was originally assumed to be appropriate for skipjack tuna, at all swimming speeds. Electromyographic (EMG) recordings from swimming skipjack tuna (Brill & Dizon MS, see footnote 5) have recently confirmed that: (1) swimming speed is indeed linearly proportional to tail beat frequency, and (2) a stride length coefficient of 0.7 is appropriate; at least over a swimming speed range of approximately 1.5 to 5.5 body lengths per second (bl s^{-1}). Whether skipjack tuna maintain a linear tail beat frequency — swimming speed relationship and a stride length coefficient of 0.7 at speeds up to 10 to 20 bl s^{-1} still await direct

confirmation. However, Watanabe (1942) and Yuen (1966) measured the maximum swimming speeds of skipjack tuna (in water of 25–27° C) as approximately 14–15 bl s^{-1} . Mean predicted maximum swimming speed at 27° C, based on a stride length coefficient of 0.7 is 14.3 bl s^{-1} . The agreement of predicted and observed values indicates the suitability of our techniques. The Yuen linear regression equation predicts maximum swimming speeds lower than those observed by Watanabe (1942) and Yuen (1966).

The mean predicted maximum swimming speed at 20° C (based on the 0.7 stride length coefficient) is 9.7 bl s^{-1} , a value equal to or less than the measured maximum swimming speeds of 40 cm salmonids in 19° C water (Weaver 1963, Blaxter 1969). Skipjack tuna are apparently not capable of exceptionally high maximum swimming speeds when compared to other teleosts of equal fork length and similar muscle temperatures.

The data presented here clearly show that increased white muscle temperature will increase maximum swimming speeds of skipjack tuna. However, skipjack tuna white muscle appears to be only slightly more temperature sensitive than white muscle of other teleosts. The maximum sustainable 1–2° C temperature difference between skipjack tuna white muscle temperature and water temperature (Dizon et al. 1978) is unlikely to have a significant effect on the maximum swimming speed of this species.

Summary

1. Latent period, rise time, contraction time, and half relaxation time from isotonic contractions of isolated white muscle samples from skipjack tuna were determined at 20°, 27°, and 34° C, and were found to be inversely proportional to temperature ($Q_{10} = 1.47, 1.67, 1.62, 1.72$, respectively).
2. The data show that the contraction time and the effect of temperature on contraction time of skipjack tuna white muscle are not unique when compared to other equal-sized teleosts.
3. Based on contraction time, maximum swimming speeds at each test temperature were calculated and found not significantly to exceed the maximum speeds of other equal-sized teleosts when comparisons are made at equal white muscle temperatures.

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Red and white muscle fibre activity in swimming skipjack tuna, *Katsuwonus pelamis* (L.)

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To test the hypothesis that white muscle fibre portions of the myotomes are used at sustainable swimming speeds, skipjack tuna, *Katsuwonus pelamis*, were forced to swim against various current velocities in a water tunnel while electrical activity of the red and white muscle fibres was simultaneously recorded. Eight fish were tested, five fish graded white muscle fibres into activity at swimming speeds above their minimum hydrostatic equilibrium speed, but well below the estimated maximum sustainable swimming speed of skipjack tuna. Three other fish showed white muscle fibre activity at minimum swimming speeds, a possibly abnormal condition.

I. INTRODUCTION

Like most teleosts, the myotomes of tuna (family Scombridae, tribe Thunnini) contain red and white muscle fibres grouped into distinct areas (Bone, 1975). However, tuna are unique because the red muscle fibre portions of the myotomes (hereafter referred to as 'red muscle fibres') are internal and make little or no contact with the body surface (Stevens *et al.*, 1974). Because of their internal position and the presence of vascular countercurrent heat exchangers, red muscle fibres in tuna are maintained significantly warmer than ambient temperature (Carey & Teal, 1966; Graham, 1975; Dizon *et al.*, 1978).

Rayner & Keenan (1967) recorded the electrical activity from the red and white muscle fibres of restrained and sedated skipjack tuna, *Katsuwonus pelamis*, and showed that red muscle fibres alone were active during low frequency swimming movements. White muscle fibres showed activity only at the higher tail beat frequencies caused by tactile stimulation of the head and operculum. Based on their results, Rayner & Keenan (1967) implied that skipjack tuna use red muscle fibres at sustainable swimming speeds and white muscle fibres only at unsustainable burst speeds. However, because Rayner & Keenan (1967) used restrained skipjack tuna, red and white muscle fibre activity could not be correlated with specific swimming speeds. A growing body of evidence now indicates that

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numerous teleost species employ their white muscle fibres at sustainable speeds. This has been demonstrated by: (a) direct electromyographic recording (Hudson, 1973; Davison *et al.*, 1976; Johnston *et al.*, 1977; Bone *et al.*, 1978), (b) hypertrophy of each muscle fibre type (Greer-Walker, 1970; Greer-Walker & Pull, 1973), (c) metabolite depletion (Pritchard *et al.*, 1971; Johnston & Goldspink, 1973a, 1973b), and (d) apparent increases in swimming efficiency (Smit, 1965; Smit *et al.*, 1971). Hochachka *et al.* (1978) have shown that the white muscle fibres in skipjack tuna have the enzymatic capacity to sustain significant levels of aerobic metabolism. It is possible (as suggested by Bone *et al.*, 1978) that skipjack tuna may also employ white muscle fibres at sustainable swimming speeds. Furthermore, this may have a thermoregulatory function in tuna (Dizon & Brill, 1979). Our study was therefore undertaken to find at what swimming speeds the white muscle fibres of skipjack tuna become active, by forcing fish to swim against various current velocities in a water tunnel.

II. MATERIALS AND METHODS

The water tunnel was a 20-cm diameter polyvinyl chloride (PVC) pipe fitted with a curved plexiglass access hatch. Stainless steel screens constrained the fish within a 1-m long test section. The upstream end of the tunnel was attached to a port approximately 1 m below the surface of a 120 000-l oceanarium. Water flow through the tunnel was due to gravity and was controlled by a butterfly valve located downstream of the test section. Maximum water velocity was approximately 160 cm s^{-1} .

Water velocity was measured with a ducted impeller current meter (Marine Advisors Inc.*). The ducted impeller was mounted behind the test section rear screen, but upstream of the butterfly valve.

Red and white muscle fibre activity was simultaneously recorded using two pairs of bipolar electrodes consisting of the bared tips of four strands of insulated 30 AWG silver plated copper wire. The wires were inserted in a 6 cm length of 2 mm diameter polyethylene (PE) tube. The red muscle electrodes protruded from the end of the tube, and the white muscle electrodes 4 cm distally.

Muscle fibre electrical activity was amplified by two Tectronix 122 low level differential preamplifiers, displayed on a Tectronix 502A dual beam oscilloscope and recorded on a Beckman R421 Dynograph recorder.

Skipjack tuna were selected from stocks maintained at the Kewalo Research Facility of the National Marine Fisheries Service. Nakamura (1972) provides details on handling of tuna at this facility. An animal was removed from its holding tank, transferred to the water tunnel, and immediately outfitted with muscle activity electrodes. The PE tube, containing the electrodes, was pushed into a puncture wound made about 1 cm laterad and slightly posterior to the origin of the first dorsal fin. The fish was then rested for 20–30 min at water velocities at or below its estimated minimum hydrostatic equilibrium speed (Magnuson, 1978). To determine at what speed white muscle fibres become active, current velocity was slowly increased until maximum water velocity was reached, and then decreased until the fish was again swimming at its minimum swimming speed. Periods of elevated water velocity were alternated with 15–30 min rest periods, as long as a fish showed good stamina.

At the end of each experiment, the fish was killed. The exact electrode position was then confirmed by dissection. White muscle electrodes were generally found 0.5–1 cm below the dorsal body surface, and the red muscle electrodes immediately lateral to the vertebral column.

*Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Because the effective cross sectional area of the tunnel is reduced due to solid blocking by the fish, the measured water velocity (U_m) is less than the velocity of the water as it passes the fish. This velocity (U_c , assumed equal to the fish's swimming speed) was calculated by

$$U_c = \frac{S_t}{S_t - S_b} \cdot U_m \quad (\text{Webb, 1975})$$

where: S_t = cross sectional area of the tunnel, S_b = maximum cross sectional area of the fish. Velocity correction factors are listed in Tables I and II.

TABLE I. Swimming speeds at which white muscle fibres become active (during increasing speed) and inactive (during decreasing speed)

Fish No.	Fork length (cm)	Velocity correction factor	Test No.	Swimming speed at which white muscle fibres become active		Swimming speed at which white muscle fibres become inactive	
				cm s ⁻¹	bl s ⁻¹	cm s ⁻¹	bl s ⁻¹
1	50.6	1.37	1	187	3.69	172	3.40
			2	151	2.99	190	3.75
			3	187	3.69	193	3.82
			4	197	3.89	200	3.96
			5	190	3.75	187	3.70
			6	207	4.10	204	4.03
2	49.0	1.34	1	210	4.29	175	3.58
3	48.5	1.33	1	174	3.59	205	4.23
			2	219	4.51	212	4.38
			3	202	4.16	202	4.16
			4	212	4.38	205	4.23
			5	266	5.49	stopped swimming	
4	38.2	1.13	1	148	3.88	64	1.67
5	40.1	1.17	1	150	3.74	123	3.08
			2	162	4.05	204	5.10
			3	190	4.73	168	4.20

TABLE II. Range of swimming speed at which red and white muscle fibres were active in Fish 6-8

Fish No.	Fork length (cm)	Velocity correction factor	Range of swimming speeds at which white muscle fibres were active	
			cm s ⁻¹	bl s ⁻¹
6	39.2	1.15	59- 86	1.51-2.19
7	40.1	1.17	78- 81	1.95-2.12
8	50.0	1.36	77-113	1.54-2.26

III. RESULTS

ELECTROMYOGRAPHIC RECORDINGS

Plate I presents the complete electromyographic recording made from Fish 1, during test 5 (Table I). Red muscle fibre activity is shown in the upper trace,

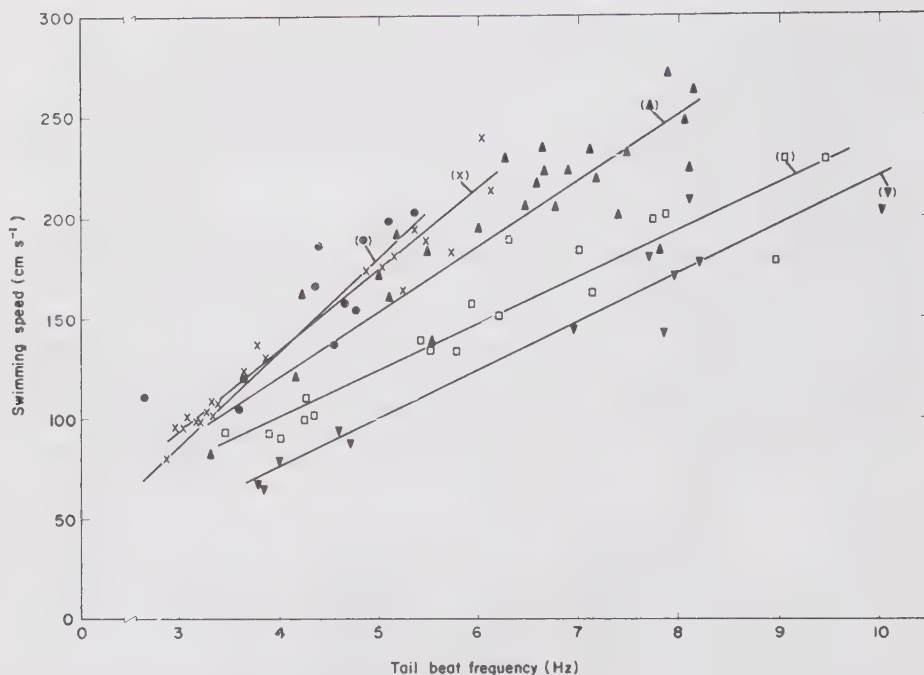


FIG. 1. A plot of tail beat frequency (Hz) versus swimming speed (cm s^{-1}), for fish 1–5 (x, ●, ▲, ▼, and □, respectively). The lines were fitted by a linear least squares regression.

white muscle fibre activity in the lower trace. The increasing amplitude of the upper trace, with increasing speed, is assumed to be due to red muscle fibre recruitment (Grillner & Kashin, 1976). The smaller spikes in the lower trace, seen at slower swimming speeds, are also assumed to reflect red muscle fibre activity. White muscle fibre action potentials begin at a swimming speed of 190 cm s^{-1} (arrow, Plate I). White muscle fibre use clearly increases and decreases with water velocity. At swimming speeds below 187 cm s^{-1} (arrow, Plate I), white muscle fibre activity ceases.

The four other fish that were tested at higher water velocities demonstrated red and white muscle fibre activity patterns similar to Plate I. The swimming speeds at which white muscle fibres commenced and ceased activity are listed in Table I.

In contrast, three skipjack tuna (Fish 6, 7, and 8) demonstrated white muscle fibre activity at swimming speeds near their minimum hydrostatic equilibrium speeds (Table II). Fish 7, shown in Plate II, employed its white muscle fibres at swimming speeds as low as 78 cm s^{-1} . Neither Fish 6, 7, nor 8 had good stamina. They could not maintain their position in the water tunnel against current velocities above approximately 113 cm s^{-1} .

TAIL BEAT FREQUENCY VERSUS SWIMMING SPEED

Above a minimum swimming speed, most teleosts show a linear relationship between tail beat frequency and swimming speed (Bainbridge, 1958; Hunter & Zweifel, 1971; Hudson, 1973). As a rough indication of the normal pattern of the

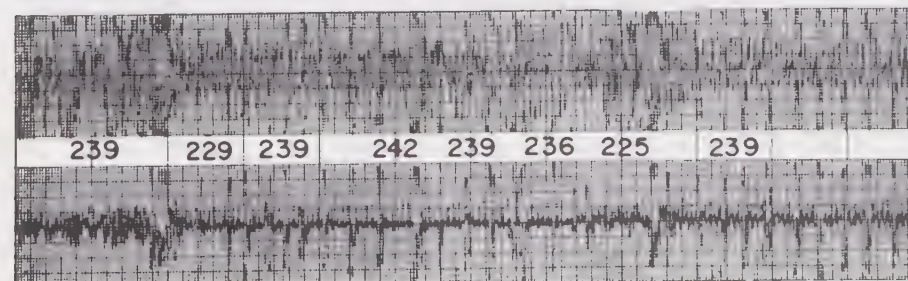
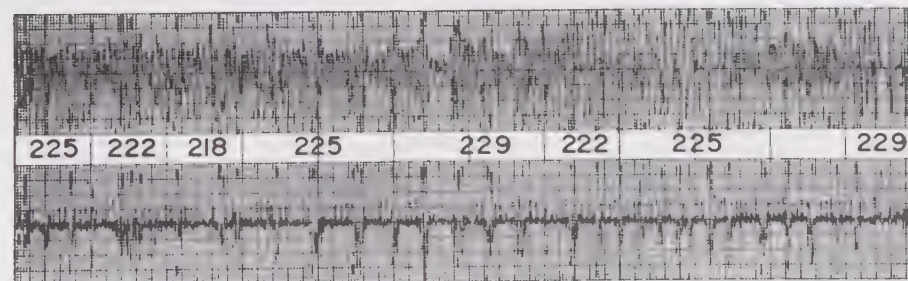
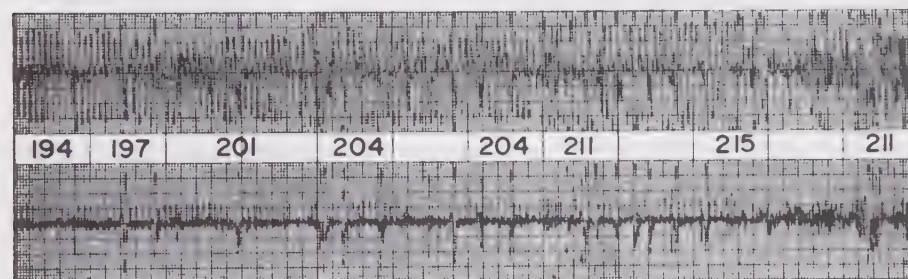
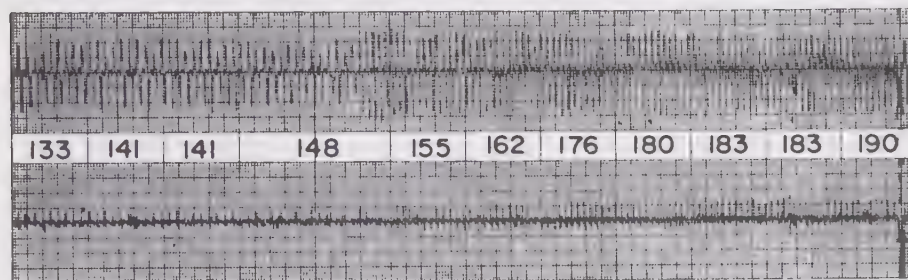
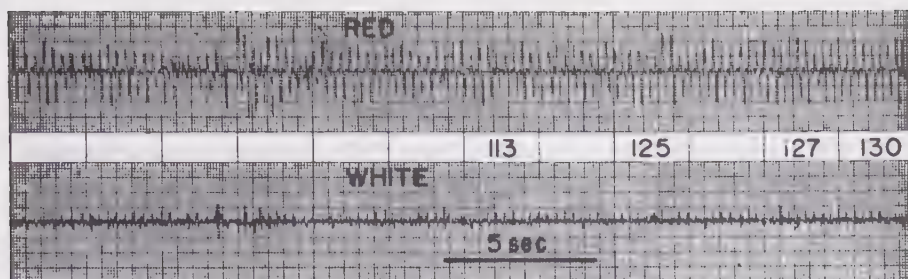


PLATE I(a).

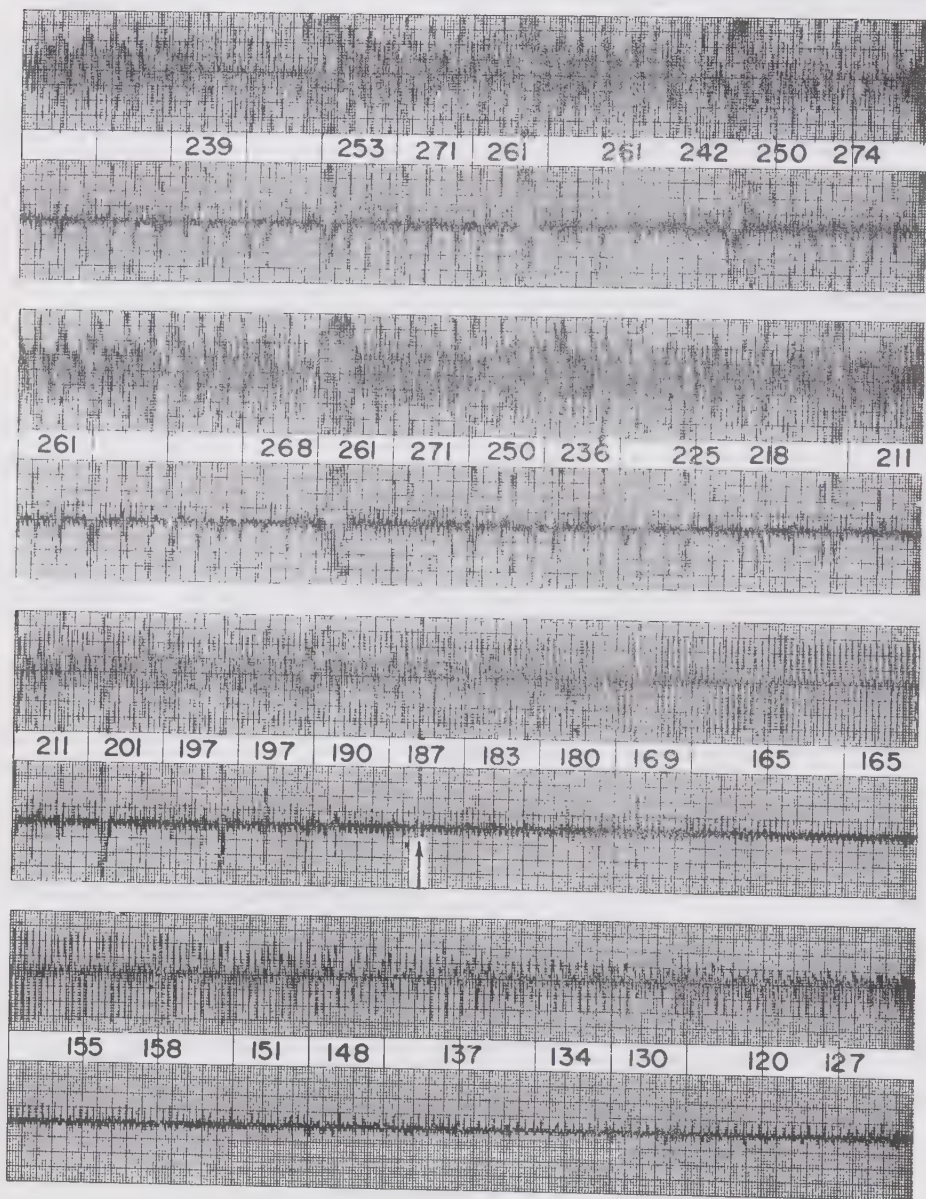


PLATE I(b).

PLATE I. The complete electromyographic record for Fish 1, during test 5. Red muscle activity is shown in the upper trace, white muscle activity in the lower. The numbers indicate swimming speed (cm s^{-1}). The activity seen in the lower trace, at the slower swimming speeds, is assumed to represent red muscle activity. White muscle activity (large amplitude traces) begins at 190 cm s^{-1} (arrow) and ceases at 187 cm s^{-1} (arrow). Chart speed is shown by a horizontal line at the start of the record.

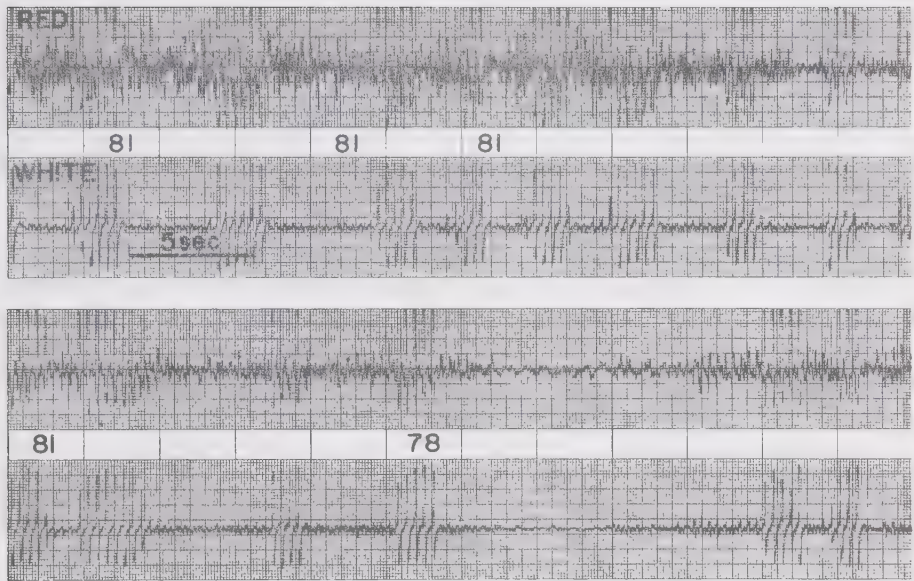


PLATE II. An electromyographic record from Fish 7. Note the use of white muscle fibres (lower trace) at slow swimming speeds. The numbers indicate swimming speed (cm s^{-1}); chart speed is indicated by a horizontal line.

TABLE III. Linear regression parameters for swimming speed (cm s^{-1}) and tail beat frequency (Hz), the means and ranges of stride length coefficients are also given

Fish No.	<i>n</i>	Intercept	Slope ($\pm$ 95% confidence limits)	Coefficient of determination	Mean stride length coefficient	Range
1	25	-26.98	40.20 $\pm$ 3.56	0.96	0.66	0.56-0.78
2	11	-13.85	38.85 $\pm$ 15.77	0.78	0.72	0.61-0.86
3	25	8.39	30.45 $\pm$ 6.06	0.82	0.65	0.50-0.77
4	12	-20.39	24.22 $\pm$ 4.99	0.92	0.54	0.45-0.67
5	18	10.10	22.85 $\pm$ 4.27	0.89	0.61	0.50-0.74

swimming of the fish in our water tunnel, we regressed tail beat frequency on swimming speed, based on the electromyographic records from fish 1-5. Each upward pen deflection was considered one tail beat. The number of tail beats within 2-10 s were sampled from those portions of the records where tail beat frequency was more distinct. In all cases, the slope of the regression line was significantly different from zero (Fig. 1, Table III). The regression of swimming speed on tail beat frequency was able to account for 78% to 96% of the observed variation of swimming speed (coefficient of determination, Table III). Furthermore, only fish 4 (Table III) had a mean stride length coefficient (i.e. the fraction of body length travelled per complete tail beat cycle) that fell outside the range of stride length coefficients found for other teleosts (0.6-0.8, Bainbridge, 1958). These data imply that the water tunnel used in this study is suitable, because the tail beat frequency—swimming speed relationship—remained normal.

IV. DISCUSSION

The data clearly show that white muscle fibres of skipjack tuna are graded into activity far below maximum swimming speed (15-20 bl s^{-1} at the water temperatures used in this study, Brill & Dizon, 1979), and are also used at speeds below the estimated maximum sustainable speed for this species (6 bl s^{-1} , Dizon *et al.*, 1978). Also, the white muscle fibres function in such a way that when they do become active they do not change the linear relationship of tail beat frequency and swimming speed (Fig. 1) during either periods of increasing or decreasing swimming speed.

Hudson (1973), Bone (1975), and Bone *et al.* (1978) have suggested that in certain teleosts the polyeuronally innervated white muscle fibres may function even at very slow swimming speeds, through local contractions initiated by junctional potentials which are below the threshold for initiation of spike potentials. We interpret the electrical activity appearing in the white muscle trace (Plate I) at slow swimming speeds to be an overlap of electrical activity from the red muscle fibres. Conceivably, our recording techniques may have failed to detect local contractions of white muscle fibres. Still, we feel our data support the hypothesis of Rayner & Keenan (1967), that white muscle fibres are not normally used at very slow swimming speeds.

Plate II shows a skipjack tuna displaying white muscle fibre activity at very slow swimming speeds. We believe these data represent an abnormal condition, based on the following line of reasoning: the efficiency (i.e. work output per quantity of ATP hydrolyzed) of isolated muscles has been shown to be maximized at a given speed of shortening. Muscle efficiency falls away sharply at speeds other than the maximally efficient speed (Goldspink, 1975). The speed of shortening of an unloaded muscle has been shown to be proportional to its myofibrillar ATPase level (Barany, 1967). Therefore, the speed of contraction at which a muscle is most efficient is also linked to its myofibrillar ATPase level. Because the myofibrillar ATPase level in skipjack tuna white muscle is likely to be about twice that in the red muscle fibres (Johnston & Tota, 1974), white muscle fibres must be inefficient if they are used at very slow swimming speeds. Thus we suspect that white muscle fibres are not normally active at very slow swimming speeds, as in Fish 6–8. However, our data do show that, like other teleosts, skipjack tuna grade their white muscle fibres into activity at apparently sustainable swimming speeds.

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THE NOMEID GENUS *CUBICEPS* (PISCES) WITH A DESCRIPTION OF A NEW SPECIES

John L. Butler

ABSTRACT

Seven species of *Cubiceps* are recognized, based on dentition, the position of predorsal bones, and meristics. Teeth on the vomer are uniserial in *Cubiceps baxteri* McCulloch, *C. capensis* (Smith), and *C. squamiceps* (Lloyd). There is a broad knobby patch of vomerine teeth in *C. caeruleus* Regan, *C. gracilis* Lowe, and *C. pauciradiatus*. Teeth are absent on the vomer in *C. paradoxus* new species. The position of the predorsal bones in *C. caeruleus* and *C. gracilis* is unique among nomeids.

Fishes of the nomeid genus *Cubiceps* are important oceanic fishes in the temperate and tropical oceans. They are routinely found in the stomachs of porpoises (Perrin et al., 1973; Fitch, pers. comm.) and tunas (Alverson, 1963; Legand et al., 1972). Large specimens are occasionally taken on tuna longlines (Abe, 1955) and in the Philippine lift net fishery (Herre and Herald, 1950). A potential fishery may exist off South Africa where a trawler reported taking up to 10 tons in a purse seine (Elizabeth Louw, pers. comm.). Only a few specimens were preserved; the remainder of the catch was dumped for lack of a market.

In spite of the apparent abundance of the species, specimens in museums are few and comparative material has only recently been available. The original descriptions of several species have been inadequate or even misleading. The species are all quite similar, and most have wide distributions. This has led to considerable confusion. Early workers have either described new material as new species, or have assigned new records to the type of the genus. Thus, *C. pauciradiatus* Gunther, a worldwide tropical species, has four junior synonyms from various localities, whereas specimens from around the world have been identified as *C. gracilis* Lowe, a species restricted to the northwestern Atlantic and Mediterranean.

In his revision of the stromateoid fishes Haedrich (1967) defined the genus and gave tentative synonymies for the species. In 1972, working with adult specimens, Haedrich further characterized the genus by the squamation on top of the head. In 1976 Ahlstrom et al. described life histories of five species of *Cubiceps*, two of which were considered as possibly undescribed species. They designated these two kinds as *Cubiceps* sp. A and *Cubiceps* sp. B. Since these species had unusual caudal fin counts, radiographs were obtained of the types of likely nominal species. Study of radiographs of the stuffed holotype of *C. capensis* (Smith) showed clearly that it possessed the high procurent ray count and meristics characteristic of *Cubiceps* sp. A of Ahlstrom et al. (1976). Additional specimens of this species from off South Africa had a predorsal formula of 0/0/0+2/. This form is quite distinct from the one that Haedrich (1967) had described as *C. capensis*. Radiographs and subsequent study of the two small cotypes of *C. caeruleus* Regan showed that this species has the predorsal formula of 0/0/0/2/, two rather than three anal spines and knobby teeth on the vomer. Hence this is actually the species which Haedrich (1967, 1972) and Ahlstrom et al. (1976) had assigned to *C. capensis*. The problem remained as to which name, if any, applied to the species that had been called *C. caeruleus* by Haedrich (1967, 1972) and by Ahlstrom et al. (1976). A radiograph of the holotype of *C. baxteri* McCulloch



Figure 1. Arrangement of predorsal bones (black), first four dorsal pterygiophores (shaded), and first six neural spines (unshaded) in *Cubiceps caeruleus* and *C. gracilis*.

showed it to be conspecific with *C. caeruleus* of Haedrich (1967, 1972) and Ahlstrom et al. (1976) and that the species should therefore be known as *C. baxteri*.

Hence, based on the findings of this study, the names applied to the several species of *Cubiceps* are markedly changed. Of the five species treated by Ahlstrom et al. (1976), the nomenclature should be revised as follows: *C. caeruleus* = *C. baxteri*, *C. capensis* = *C. caeruleus*, *Cubiceps* sp. A = *C. capensis* and *Cubiceps* sp. B is described as a new species *C. paradoxus*. Only *C. pauciradiatus* remains unchanged.

MATERIALS AND METHODS

Specimens examined in this study are housed in the following institutions: Australian Museum, Sydney (AM), British Museum—Natural History (BMNH), Institute für Seefischerei, Hamburg (ISH), Natural History Museum of Los Angeles County, Los Angeles (LACM), National Museum, New Zealand (NMNZ), J. L. B. Smith Institute of Ichthyology, Rhodes University (RUSI), South African Museum, Capetown (SAM), Scripps Institution of Oceanography (SIO), National Museum of Natural History, United States (USNM), University of Washington (UW), and Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, California (SFC) (SFC numbers are station numbers, not catalogue numbers).

Measurements are self explanatory. Vertebrae, predorsal bones, dorsal, anal and caudal fin elements were counted from radiographs. The relation of predorsal bones, neural spines, and pterygiophores is expressed as the following formula: predorsal bones are designated as 0, neural spines as 1, and the first pterygiophore as 2 (Ahlstrom et al., 1976).

Cubiceps Lowe, 1843

Diagnosis.—Elongate nomeids with scales covering the top of the head almost to the nostrils, origin of dorsal fin over or behind pectoral fin base (Haedrich, 1972), larvae without early developing pelvic fins, and juveniles not conspicuously barred (Ahlstrom et al., 1976). Allometric growth of pectoral fin in several species, the pectoral fin becoming longer in adults. Vomerine, glossohyal and palatine teeth usually present. Predorsal bones in two patterns. One pattern with the first predorsal bone in advance of the first neural spine, the second predorsal between the first and second neural spines, the third predorsal between the second and



Figure 2. *Cubiceps baxteri*, McCulloch, Lord Howe Island, BMNH 1926, 6.30.50. 276 mm.

third neural spines, and the first pterygiophore between the third and fourth neural spines 0/0/0/2/ (Fig. 1). This pattern is found in *C. baxteri*, *C. capensis*, *C. squamiceps*, *C. pauciradiatus*, and *C. paradoxus*, n. sp.

ARTIFICIAL KEY TO THE SPECIES OF *CUBICEPS*

- | | |
|---|--|
| 1a. Teeth on vomer in broad knobby patches | 2 |
| 1b. Teeth on vomer uniserial or lacking | 4 |
| 2a. Anal spines III, vertebrae 32-34 (33) | <i>Cubiceps gracilis</i> Lowe 1843 |
| 2b. Vertebrae 31, anal spines II | 3 |
| 3a. Dorsal soft rays 15-17, anal rays 14-16 | <i>Cubiceps pauciradiatus</i> Günther 1872 |
| 3b. Dorsal soft rays 23-27, anal rays 23-24 | <i>Cubiceps caeruleus</i> Regan 1914 |
| 4a. Upper procurent caudal rays 8-10 | 5 |
| 4b. Upper procurent caudal rays 11-12 | 6 |
| 5a. Dorsal soft rays 20-23, anal rays 20-22, vertebrae 12 + 19 = 31 | <i>Cubiceps baxteri</i> McCulloch 1923 |
| 5b. Dorsal soft rays 17-20, anal rays 17-19, vertebrae 13 + 18 = 31 | <i>Cubiceps squamiceps</i> (Lloyd) 1909 |
| 6a. Teeth on tongue uniserial | <i>Cubiceps capensis</i> (Smith) 1849 |
| 6b. Teeth on tongue lacking | <i>Cubiceps paradoxus</i> new species |

Cubiceps baxteri McCulloch (Figure 2)

Cubiceps baxteri McCulloch, 1923, 14: 15, pl. 1. Holotype in Australian Museum.

Cubiceps caeruleus, not of Günther, McCulloch, 1923, 14: 15, pl. 1; Haedrich, 1967, 40, 81 (in part, Lord Howe Island specimen only); Haedrich, 1972, pp. 77-79; Ahlstrom et al., 1976, pp. 339-342.

Cubiceps gracilis, not of Lowe, Abe 1955, pp. 1-5; Smith, 1966, pp. 65-69.

Material.—Australia and Lord Howe Island: AM, Holotype, radiograph only; AM 7585, 1 (418 mm); AM 17598, 1 (415 mm); AM 16150, 1 (283 mm); BMNH 1926, 6.30.50, 1 (276 mm). Eastern tropical Pacific: SIO 77-231, 4 (92-110 mm); SIO 77-227, 3 (79-165 mm); SIO 77-229, 1 (157 mm); SIO 75-257, 4 (110-129 mm); SIO 75-253, 1 (120 mm). South Atlantic: ISH 1391/68, 1 (127 mm); ISH 1449/68, 1 (135 mm).

Additional Material.—An additional 283 specimens in 29 lots from the eastern Pacific were seen.

Diagnosis.—A *Cubiceps* with uniserial vomerine and glossohyaline teeth, 20-23 soft dorsal rays and 19-22 soft anal rays. The pectoral fin is longer than the head in specimens longer than 90 mm SL.

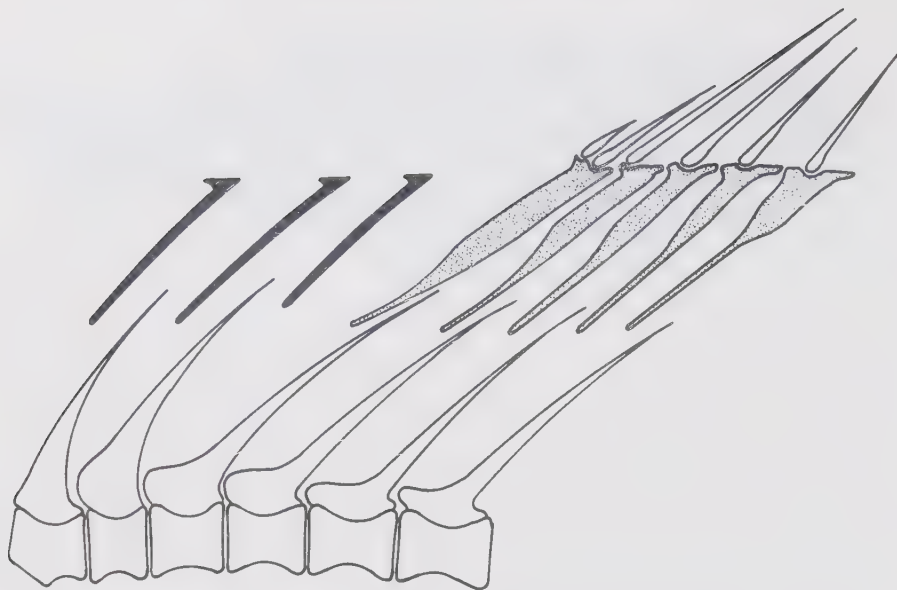


Figure 3. Arrangement of predorsal bones (black), first four dorsal pterygiophores (shaded) and neural spines (unshaded) in *Cubiceps baxteri*, *C. capensis*, *C. squamiceps* and *C. paradoxus* n. sp.

Description.—D XI, I 20–23; A III, 19–22; P 21–23; gill rakers 6–10 + 16–18, total 23–28; lateral line scales 52–66; vertebrae 12 + 19 = 31; upper procurent caudal rays 7–10; lower procurent caudal rays 7–10.

Morphometrics are given in Table 1. Body fusiform, moderately compressed. Snout blunt, top of head convex, eye of moderate size, pectoral fin exceeding length of head in specimens longer than 90 mm SL. Origin of dorsal fin slightly behind origin of pectoral fin.

Teeth on vomer, glossohyal and palatines uniserial. Third predorsal bone and first pterygiophore between second and third neural spines (0/0/0 + 2) (Fig. 3).

Color in alcohol, dark brown. Eye blue.

Size.—Specimens over 1 m in length have been reported by Abe (1955).

Remarks.—The lateral line scale count from specimens in the eastern tropical Pacific were lower than counts from specimens from the south Pacific, south Atlantic and western Pacific. In eastern tropical Pacific specimens lateral line scales numbered between 52 and 58, whereas in specimens from the south Atlantic and south Pacific, the lateral line scales numbered about 65. Specimens from the western Pacific reported by Abe also had about 65 lateral line scales. Although these counts are non-overlapping, no other difference of meristics was noted, and morphometrics of the specimens were similar. Larvae from the south central and north central Pacific do not differ from those found in the eastern tropical Pacific. Until specimens of adults from intervening areas are available, I prefer to consider the eastern tropical Pacific population to be a geographical variant of *C. baxteri*.

Identification.—*Cubiceps baxteri* was regarded as a synonym of *C. gracilis* by Smith (1966) and a synonym of *C. caeruleus* by Haedrich (1967). It is distin-

Table 1. Morphometrics of *Cubiceps* with minimum and maximum values and means in parentheses

	<i>baxteri</i>	<i>coeruleus</i>	<i>cupervisi</i>	<i>gracilis</i>	<i>pauciradiatus</i>	<i>paradoxus</i>	<i>squamiceps</i>
Number of specimens	19	39	2	4	20	1	18
Standard length (mm)	78.7-118.0	28.2-183.4	288-425	94.0-162.0	86.5-128.3	568.0	67.4-148.0
Thousands of SL							
Head length	297-364 (316)	261-365 (300)	267-293	275-320 (299)	278-332 (310)	296	304-351 (327)
Pectoral fin length	308-434 (367)	188-346 (308)	274-364	251-308 (284)	284-368 (334)	310	252-305 (272)
Pelvic fin length	108-163 (129)	104-154 (120)	169	75-113 (95)	111-143 (125)	90	154-185 (169)
Predorsal distance	321-440 (373)	202-418 (378)	321-380	358-392 (378)	346-395 (376)	354	348-376 (362)
Preanal distance	587-716 (624)	580-679 (643)	570-624	592-634 (614)	657-730 (683)	565	589-664 (638)
Maximum depth	256-351 (300)	249-344 (269)	260-280	228-283 (255)	206-278 (257)	199	292-352 (319)
Least depth caudal peduncle	89-119 (102)	72-96 (80)	89-95	77-99 (87)	87-112 (99)	65	87-106 (100)
Head length (mm)	24.4-127.3	10.3-54.0	76.9-124.6	27.7-45.5	26.0-37.1	168.0	22.8-50.0
Thousands of head length							
Snout length	226-309 (278)	243-286 (270)	266-299	222-264 (246)	250-340 (285)	323	250-292 (270)
Orbit	254-301 (278)	244-320 (276)	225-252	240-264 (250)	251-320 (282)	185	249-300 (276)
Interorbital width	203-337 (301)	262-320 (290)	247-388	278-290 (285)	257-342 (296)	271	255-333 (310)
Length of upper jaw	236-314 (276)	260-319 (295)	303-345	245-274 (262)	245-318 (268)	200	270-346 (292)

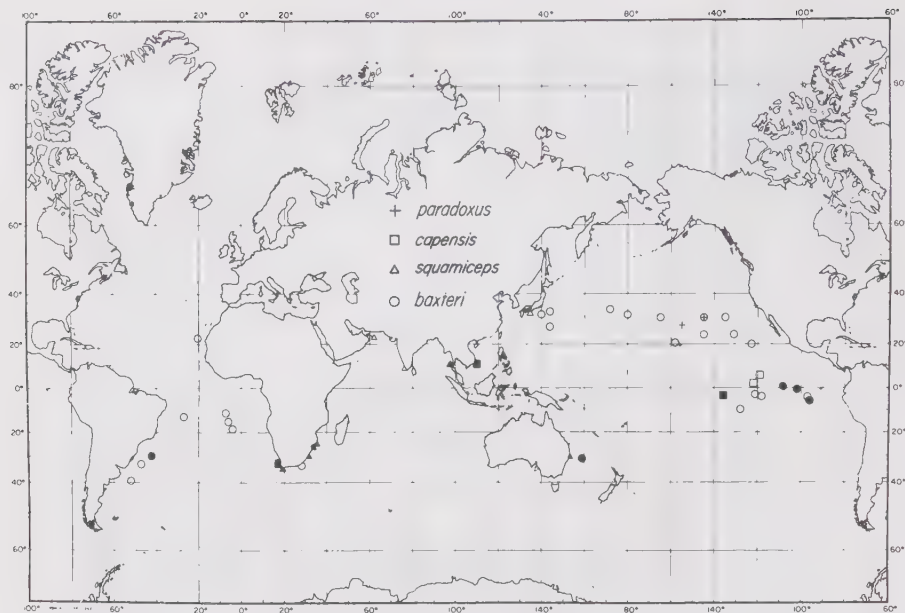


Figure 4. Distribution of *Cubiceps baxteri* (circles), *C. capensis* (squares), *C. squamiceps* (triangles) and *C. paradoxus* n. sp. (crosses). Open symbols represent literature records.

guished from both by the presence of uniserial teeth on the vomer and on the glossohyal. It is most closely related to *C. squamiceps* from which it is distinguished by its higher dorsal and anal counts and longer pectoral fin in adults.

Distribution.—*Cubiceps baxteri* is widespread in the Pacific between 35°N and 35°S (Fig. 4). It is also widespread in the Atlantic from 23°N to 40°S. A single record for the Indian Ocean is that of Smith (1966).

Cubiceps caeruleus Regan

Figure 5

Cubiceps caeruleus Regan 1914a, pp. 15–16; Regan, 1914b, lectotype BMNH 1913.12.6.29: 11–17; Trunov, 1975: pp. 351–360.

Cubiceps capensis, not of Smith, Haedrich, 1967, 135, p. 81 (in part, all non-type material); Craddock and Mead, 1970: 3.33; Haedrich, 1972: 79; Karrer, 1975: pp. 75–77; Ahlstrom et al., 1976: pp. 343–346; Pequeño, 1976: pp. 805–806.

Material.—South Pacific: BMNH 1913.12.6: 28–29. 2 (80–95 mm). Syntypes of *Cubiceps caeruleus* Regan 1914. New Zealand, Three Kings Is.; SIO 63-1008, 1 (14 mm); SIO 72-312, 1 (16 mm); SIO 77-190, 3 (155–178); NMNZ 7360 (same as SIO 77-190), 12 (161–182 mm); USNM 208082, 1 (60 mm); USNM 208086, 1 (89 mm); USNM 208083, 1 (82 mm). South Atlantic and South Africa: BMNH 1930.1.12.1072, 1 (91 mm); ISH 1200/71, 1 (142 mm); ISH 1090/71, 2 (151–162 mm); ISH 764/71, 5 (135–154 mm); USNM 206914, 4 (137–158 mm), same as ISH 764/71; RUSI 3908, 1 (160 mm); SAM 27491, 4 (28–43 mm); SAM 26069, 4 (130–133 mm); SAM 27490, 1 (42 mm); BMNH 1925.10.14.1–4, 4 (157–164 mm).

The following South Atlantic specimens of *C. caeruleus* were collected by the FFS WALTHER HERWIG, but were not available at the time of this study (G. Krefft, in litt.): WALTHER HERWIG Stas. 4-1/76, 1 (133 mm); 4-11/76, 1 (155 mm); 107/76, 1 (135 mm); 109-11/76, 1 (107 mm).

Diagnosis.—A *Cubiceps* with 23–27 dorsal rays, 21–24 anal rays, 2 anal spines,



Figure 5. *Cubiceps caeruleus*, Regan, South Atlantic, ISH 764/71. 146 mm.

a broad patch of knobby teeth on the vomer and glossohyal, and only the third predorsal bone between the second and third neural spines.

Description.—D XI, I 23–27; A II, 21–24; P 19–22, gill rakers 6–9 + 17–20, total 23–27; lateral line scales 50–56; vertebrae 12 + 19 = 31; upper procurent caudal rays 7–9; lower procurent caudal rays 7–9.

Morphometrics are given in Table 1. Body fusiform, moderately compressed.



Figure 6. Distribution of *Cubiceps caeruleus* (circles), *C. gracilis* (triangles) and *C. pauciradiatus* (squares). Open symbols represent literature records.



Figure 7. *Cubiceps capensis* (Smith), South Africa, SAM 25537. 288 mm.

Snout rounded, top of head convex, eye of moderate size. Head about 3.3 in standard length. Pectoral fin longer than head in specimens larger than 100 mm SL. Origin of dorsal fin slightly behind pectoral fin base.

Teeth on vomer and glossohyal in a broad knobby patch in specimens larger than 80 mm, uniserial in smaller specimens. About 8 to 10 teeth in a single row on palatines. A neural spine between last predorsal bone and first pterygiophore (0/0/0/2/) (Fig. 2).

Color in alcohol, dark gray with pinkish undertones in some specimens. Unscaled portion of snout bluish. Type specimens are bluish gray.

Size.—The largest specimen (182 mm) is not sexually mature.

Remarks.—A re-examination of the types of *C. caeruleus* Regan indicates several errors in the original description. The dorsal fin count is XI, 1, 25 in the larger and XI, 1, 24 in the smaller specimen (rather than XI, 1, 23). The anal fin count is II, 22 (rather than III, 21) in the larger specimen and uncountable in the smaller specimen although there are definitely only 2 anal spines. The skin is gone, so no lateral line scale count is possible. The pectoral fin has 20 rays in the larger and 21 rays in the smaller specimen. A knobby patch of teeth has formed on the glossohyal and a similar patch is beginning to form on the vomer. The third predorsal bone lies between the second and third neural spine; the first pterygiophore lies between the third and fourth neural spine (0/0/0/2/). The larger cotype, BMNH 1913.12.6.29 is here selected as the lectotype.

Distribution.—*Cubiceps caeruleus* is an antiboreal species (Fig. 6). It is widespread in the Atlantic south of 35°S. In the Pacific it reaches 19°S in the Peru Current. The absence of records from the south Indian Ocean may reflect the paucity of sampling in this region.

Cubiceps capensis (Smith)

Figure 7

Atimostoma capensis Smith 1849, pl. XXIV. Holotype in British Museum.

Cubiceps capensis, Barnard 1948, pp. 389–399, figs. 10–12. Haedrich 1967, 135, p. 81 (in part, the type only).

Cubiceps sp. A, Ahlstrom, Butler and Sumida, 1976, pp. 352–355.



Figure 8. *Cubiceps gracilis*, Lowe, Madeira, BMNH 1863, 12.12.7-8. 142 mm.

Material.—South Africa: BMNH, 1 (905 mm, stuffed), Holotype (radiograph only); SAM 19375, 1 (425 mm); SAM 25537, 1 (288 mm). Pacific Ocean: SIO 61-582, 2 (40–42 mm); SIO 71-80, 1 (19.5 mm); SIO 70-229, 1 (14 mm); SFC, ETP 11.068, 1 (8.7 mm).

Diagnosis.—A *Cubiceps* with 11–12 superior procurent caudal rays, 10–12 inferior procurent caudal rays, and uniserial teeth on the vomer.

Description.—D XI, I 20–23; A III, 20–21; P 21–23; gill rakers 7–9 + 16–19, total 23–28; lateral line scales 66–67; vertebrae 12 + 19 = 31; upper procurent caudal rays 11–12; lower procurent caudal rays 10–12.

Morphometrics are given in Table 1. Body fusiform, moderately compressed, snout convex, top of head moderately convex, eye of moderate size. Pectoral fin exceeding length of head in large specimens (>200 mm). Origin of dorsal over pectoral fin base. Caudal peduncle short.

Teeth on vomer, glossohyal, and palatines uniserial. Third predorsal bone and first pterygiophore between second and third neural spines (0/0/0 + 2/) (Fig. 3).

Color in alcohol, purplish brown, fins blackish.

Size.—The type specimen (905 mm) is the largest known.

Distribution.—South Africa and tropical Pacific (Fig. 4).

Cubiceps gracilis Lowe
Figure 8

Cubiceps gracilis Lowe, 1843.

Navarchus sulcatus Filippi and Verany, 1859.

Trachelocirrus mediterraneus Doumet, 1863.

Cubiceps lowei Osorio, 1909.

Aphareus obtusirostris Borodin, 1930.

Material.—Atlantic Ocean: BMNH 1863, 12.12.7-8, 2 (142–162 mm); ISH 58166, 2 (94–95).

Diagnosis.—A *Cubiceps* with a broad patch of knobby teeth on the vomer and glossohyal, 32–34 vertebrae and only the third predorsal bone between the second and third neural spine (0/0/0/2/) (Fig. 1).

Description.—D XI, I 21–22; A III, 20–21; P 22–23; gill rakers 7–9 + 17–18, total 24–26; lateral line scales 60–62 (from Haedrich, 1972); vertebrae 13 + 19–21 = 32–34; upper procurent caudal rays 8–9; lower procurent caudal rays 9–10.

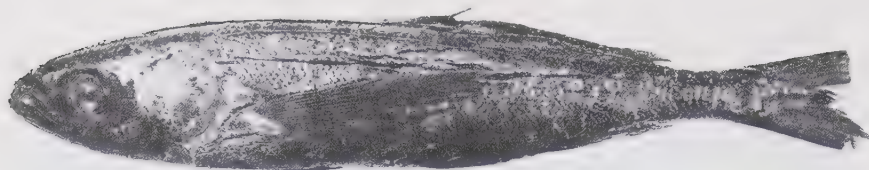


Figure 9. *Cubiceps paradoxus* n. sp. Holotype, Los Angeles, LACM 37048-1. 568 mm.

Morphometrics are given in Table 1. Body elongate, fusiform, tapering from origin of dorsal to tail. Snouth rounded, top of head sloping to dorsal. Eye of moderate size, equal to snout, about 4 in head. Head about 3.5 in SL. Pectoral fin longer than head. Origin of dorsal over pectoral base. Caudal peduncle length equal to depth.

Teeth on vomer and glossohyal in a broad knobby patch. Teeth in both jaws, conical and uniserial. No teeth on palatines.

Color in alcohol, brown.

Size.—Specimens up to 750 mm have been reported by Tortonese (1959).

Distribution.—Mediterranean and northeastern Atlantic (Fig. 6).

Cubiceps paradoxus new species

Figure 9

Cubiceps gracilis? Fitch and Lavenberg 1968, p. 118.

Cubiceps sp. B. Ahlstrom, Butler and Sumida 1976, p. 355.

Material.—Holotype, LACM 37048-1. A 568 mm malc. Taken by hook and line off Portuguese Bend, Los Angeles County, California, August 11, 1954.

Additional Pacific Ocean Material.—SFC J7210, 31.145, 1 (12.5 mm); SIO 71-310, 1 (17.9 mm); SIO 72-11, 1 (18.7 mm).

Diagnosis.—A *Cubiceps* lacking teeth on the vomer and glossohyal, with 92 lateral line scales, 11–12 upper and 11–12 lower procurent caudal rays, and a small mouth and eye.

Description.—D XI, I 19–21; A III, 20–21; P 21; gill rakers 10 + 19 = 29; lateral line scales 92; vertebrae 12 + 19 = 31; upper procurent caudal rays 11–12; lower procurent caudal rays 11–12. Hypurals 4, epurals 3.

Morphometrics are given in Table 1. Body elongate, fusiform, slightly compressed. Snout rounded, top of head tapering to dorsal profile, eye small, more than 5 in head. Snout greater than orbit, about 3 in head. Head normal, about 3.3 in SL. Pectoral fin longer than head. Origin of dorsal fin over pectoral fin base. Caudal peduncle long, length about twice depth. Caudal fin forked.

Teeth absent on vomer and glossohyal, uniserial teeth present on palatines. Third predorsal and first dorsal pterygiophore between second and third neural spines (0/0/0 + 2/) (Fig. 3).

Color in alcohol, dark brown.



Figure 10. *Cubiceps pauciradiatus*, Günther, Gulf of Aden, USNM 217365. 103 mm.

Size.—The type (568 mm) is the largest known specimen.

Etymology.—From the Latin *paradoxus*, in reference to the absence of teeth on the tongue and vomer, a character which previously was used in part to distinguish *Cubiceps* from *Psenes*.

Distribution.—North Pacific. Three juveniles from the central North Pacific and one adult from California (Fig. 4).

Cubiceps pauciradiatus Günther
Figure 10

Cubiceps pauciradiatus Günther 1872, pp. 418–426.

Cubiceps longimanus Fowler 1934, p. 442, fig. 23.

Cubiceps nesiotes Fowler 1938, pp. 195–196, pl. VIII.

Cubiceps carinatus Nichols and Murphy 1944, pp. 245–247, fig. 4.

Cubiceps athenae Haedrich 1965, pp. 501–505.

Primary synonyms only, for full synonymy see Ahlstrom et al., 1976.

Material.—Indian Ocean: USNM 217365, 1 (103 mm); USNM 217366, 1 (105 mm). Pacific Ocean: SIO 77-238, 3 (99–103 mm); SIO 75-139, 5 (91–101 mm); SIO 77-229, 2 (122–125 mm); SIO 75-103, 5 (105–122 mm); AM 117876-010, 2 (86–105 mm). Atlantic Ocean: SAM 23760, 1 (128 mm).

Additional Material.—Used only for distribution. Atlantic Ocean.—Fred Berry 057-3307.N9, off North Carolina, 1 (7.5 mm). Indian Ocean.—Dodo VI (SIO), Sta. 5, 1 (5.5 mm); Sta. 20, 4 (3.5–7.2 mm); Sta. 22, 3 (6.4–7.8 mm); Sta. 27, 6 (3.5–7.0 mm); Sta. 47, 2 (4.6–6.5 mm); Sta. 64, 2 (5.0–6.1 mm); Sta. 78, 1 (3.5 mm). Pacific Ocean.—SIO 70-103, 1 (8.2 mm); SIO 72-9, 1 (14.2 mm); SIO 61-595, 1 (12 mm); SIO 61-572, 1 (10.5 mm); SIO 61-744, 1 (26.5 mm). An additional 416 specimens in 55 lots from the eastern Pacific were seen.

Diagnosis.—The small number of dorsal and anal rays, the patches of knobby teeth on the vomer and on the glossohyal, the two anal spines, and the bony keel on the breast distinguish this species from all other nomeids.

Description.—D (X)XI, I 15–17; A II, 14–16; P 17–20; gill rakers 7–9 + 16–19, total 22–26; lateral line scales 49–53; vertebrae 12 + 19 (18) = 31 (30); upper precurrent caudal rays 8–10; lower precurrent caudal rays 8–10.



Figure 11. *Cubiceps squamiceps* (Lloyd), New South Wales, AM-I190902. 129 mm.

Morphometrics are given in Table 1. Body fusiform, compressed, snout rounded, top of head convex, eye of moderate size, equal to snout, about 3.3 in head. Head about 3.5 in SL. Pectoral fin longer than head in specimens larger than 90 mm SL. Origin of dorsal fin slightly behind pectoral fin base. Caudal peduncle short, about as long as wide.

Teeth on vomer and glossohyal in a broad knobby patch. Palatine teeth reduced to one or two teeth on each side or absent in some specimens. Both the third predorsal and the first pterygiophore between the second and third neural spines (0/0/0 + 2/) (Fig. 3).

Color in alcohol, brown above, yellowish tan on sides and belly. Fins hyaline.

Size.—This species may not exceed 200 mm in length.

Distribution.—Cosmopolitan in tropical and sub-tropical seas between 40°N and 40°S (Fig. 6). For additional records in the eastern tropical Pacific see Ahlstrom et al. (1976).

Cubiceps squamiceps (Lloyd)

Figure 11

Mulichthys squamiceps Lloyd 1909, pp. 139–180. Holotype in Indian Museum, Calcutta. Kamohara 1952, p. 36.

Cubiceps natalensis Gilchrist and Von Bonde 1923: pp. 7–8, fig. 2, no types designated. Tholasilangam et al., 1964, p. 178, fig. 6. Kamohara, 1952, p. 35.

Cubiceps gracilis, not of Lowe, Herre and Herald 1950, p. 7.

Material.—Philippine Islands: UW 7168, 2 (111–127 mm); UW 7169, 2 (138–144 mm). South Africa: SAM 9991, 1 (67 mm); SAM 26973, 2 (115–138 mm). Australia: AM-I190902, 6 (127–148 mm); AM 15970, 1 (85.5 mm); AM 17874, (73.3 mm); AM 16572, 1 (126.8 mm); AM 17862, 1 (143.2 mm); AM 17884, 1 (137.1 mm). Indian Ocean: IIOE ANTON BRUUN Cruise 1, Sta. 22, 15 (111–123 mm)—radiograph only; IIOE ANTON BRUUN Cruise 8, Sta. 396B, 7 (62–135 mm)—radiograph only.

Diagnosis.—A *Cubiceps* with uniserial teeth on the vomer, 18–19 anal rays, 18–20 pectoral rays and the pectoral fin shorter than the head.

Description.—D (X)XI, I 18–21; A III, 18–20; P 18–20; gill rakers 6–9 + 16–19,

total 23–28; lateral line scales 56–63; vertebrae $13 + 18$ (19) = 31 (32); upper precurrent caudal rays 8–9; lower precurrent caudal rays 8–9.

Morphometrics are given in Table 1. Body fusiform, laterally compressed, greatest depth behind pectoral fin base. Snout rounded, top of head sloping to nape. Eye of moderate size, equal to snout about 3.5 in head. Head about 3 in SL. Pectoral fin less than head in specimens 145 mm in SL. Origin of dorsal over insertion of pectoral fin. Origin of pelvics slightly behind pectoral fin base. Caudal peduncle short, length about equal to depth.

Teeth in both jaws, vomer, glossohyal and palatines, conical and uniserial. A few teeth on head of vomer. Third predorsal bone and first pterygiophore between second and third neural spines (0/0/0 + 2/) (Fig. 3). Fine scales on top of head but snout and preorbital space naked.

Color in alcohol, brown shading to tan ventrally, fins dusky.

Distribution.—Indo-West Pacific, South Africa, India, Japan, Philippine Is., and Australia (Fig. 4). All collections have been taken in relatively shallow water. *Cubiceps squamiceps* appears to be a coastal species in an otherwise oceanic genus.

Otoliths

Sagittae of four species of *Cubiceps* were available for this study (Fig. 12). The otoliths of *C. baxteri* and *C. gracilis* are remarkably similar. Both otoliths have a distinct rostrum and a small antirostrum. The ostium is broad and the cauda narrow. The cauda bends ventrally near the posterior end. In *C. baxteri* the antirostrum is more developed, the anterior ventral margin smooth rather than serrate. The ratio of standard length to otolith length is 15.8:1; the ratio of otolith length to height is 1.5:1. The otoliths of *C. gracilis* were illustrated by Chaîne (1958). The otolith illustrated here was donated to J. Fitch by C. Karrer. The ratio of standard length to otolith length is 17.4:1 and the ratio of otolith length to height is 1.8:1. The otolith of *C. paradoxus* is quite different from those of the other species. The margins are almost smooth, there is no antirostrum development and the narrow sulcus is nearly straight. The ratio of standard length to otolith length is 19.2:1 and the ratio of otolith length to height is 2.0:1. The otolith of *C. pauciradiatus* is smaller and more oval in outline than otoliths of the other species. The ratio of standard length to otolith length is 21.1:1 and the ratio of otolith length to height is 2.3:1. The posterior dorsal angle is notched. The sulcus is broad and the cauda bends ventrally. An otolith of *C. pauciradiatus* was illustrated from the stomach of the delphinid *Stenella graffmani* = *S. attenuata* as Centrolophidae? by Fitch and Brownell (1968).

DISCUSSION

The presence of teeth on the vomer and palatines has been thought to characterize all nomeids (Haedrich, 1967). However, vomerine teeth are absent in *C. paradoxus* and palatine teeth could not be found in *C. gracilis*. Although this alters the diagnosis of the family it does not indicate that any realignments of, or within, the family are necessary.

Developmental series are known for at least six and probably all seven species of *Cubiceps*. The developmental series of *C. gracilis* was described by Sparta (1946). Ahlstrom et al. (1976) described complete developmental series for *C. pauciradiatus*, and for *C. baxteri* which was then called *C. caeruleus*. Ahlstrom et al. (1976) had a less complete series for *C. caeruleus* (then called *C. capensis*), *Cubiceps* sp. A (presently known to be *C. capensis*), and *Cubiceps* sp. B (herein

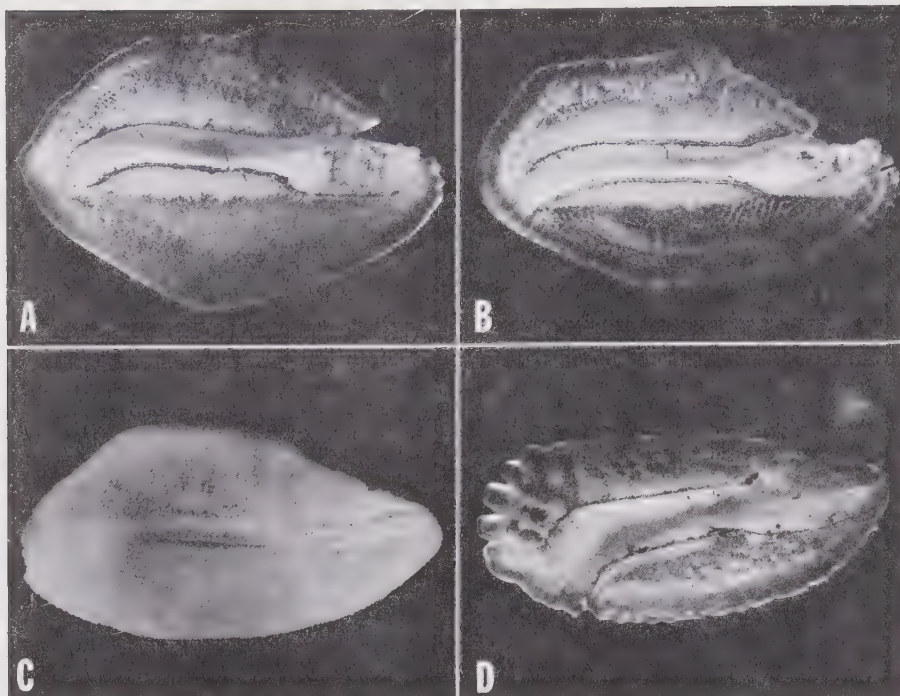


Figure 12. Median views of otoliths, anterior end to the right. A. *Cubiceps baxteri*, SIO 77-227, otolith 10.5 mm, specimen 166 mm; B. *Cubiceps gracilis*, N.W. Africa, otolith 9.3 mm, specimen 162 mm; C. *Cubiceps paradoxus* n. sp. Holotype, otolith 29.5 mm, specimen 568 mm (right otolith, negative reversed); D. *Cubiceps pauciradiatus* SIO 77-227, otolith 5.9 mm, specimen 125 mm.

described as *Cubiceps paradoxus*). Nellen (1973) illustrated an 8.8-mm TL larva of a nomeid, as *Psenes whiteleggii*, which almost certainly is the larva of *Cubiceps squamiceps*.

Trunov (1975) reported specimens of putative *Cubiceps* (designated *Cubiceps* sp.) with knobby teeth on the vomer and scales covering the entire head including the snout. I have not seen any specimens which fit his description. Additional study including vertebral numbers and predorsal bone arrangement is necessary to place these specimens.

Among the species, no clear lineage is evident. The species with knobby vomerine teeth could be considered a derived group with *C. caeruleus* and *C. pauciradiatus*, each having lost one anal spine, the most derived. *Cubiceps gracilis* with knobby vomerine teeth and increased numbers of vertebrae has an otolith remarkably similar to that of *C. baxteri*. Both *C. baxteri* and *C. squamiceps* appear to be central among the species. They have three anal spines and uniserial vomerine teeth. *Cubiceps capensis* is near *C. baxteri* and *C. squamiceps* but shares the high number of procurrent caudal rays with *C. paradoxus*. The loss of vomerine dentition in *C. paradoxus* represents a derivation which parallels that of the arriomids.

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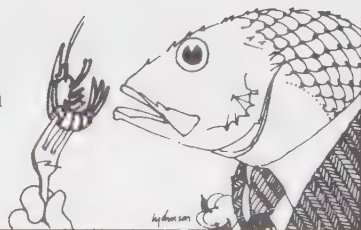
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Some Procedures for Assessing Organisms Associated with Rocky Substrata

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Studies of food habits in fishes are more meaningful if they determine not only what the fishes eat but also measure the prey that are potentially available to them. This is particularly important in studies that consider competition and feeding selectivity among predators. To measure potentially available food, or to determine if a resource becomes limiting, one must take consistent and quantitative samples of the biota within the feeding area. Furthermore, to evaluate the selectivity of a predator, one must consider organisms that are not preyed upon along with those that are.

An investigation of prey availability must also consider both temporal and spatial variations in density and distribution. Temporal variations, including seasonal changes and differences in distributions between day and night, can be profound, and understanding their patterns is important in determining how resources are utilized (Hobson and Chess, 1976).

It is a major task to monitor potentially available prey owing to the tremendous numbers and variety of organisms involved. Taxonomic problems are especially frustrating since many invertebrate groups, including the gammaridean amphipods and ostracods, are either difficult to work with, or poorly known, or both. Furthermore, to fully understand the interspecific relationships, taxa must be distinguished to species, and this is complicated by the fact that our knowledge of the systematics of many groups remains incomplete.

It is important to remember, however, that the availability of a given prey is not determined simply by its abundance. Availability is also determined by the predator's feeding strategy as well as the behavior and morphology of the prey. Thus studies of prey behavior should be an integral part of a comprehensive evaluation of food habits in fishes.

Background

The techniques described here, among others, were developed to monitor a variety of marine communities during comprehensive studies of feeding activities in fishes at Catalina Island, California (Hobson and Chess, 1976; Hobson and Chess, in prep.) Some of the same techniques are now being used in studies on the coast of northern California. This report considers methods developed to assess the organisms associated with rocky substrata accessible to divers using compressed air.

Selecting and Marking Study Sites

Preliminary surveys are important in selecting specific locations that characterize the general study area. Although it may be self-evident that data must be collected from a site that typifies the habitat under study, some investigators fail to meet this basic requirement. Study sites are usually selected on the basis of dominant or persistent floral components or type of substrata. Once the site is selected, spikes or stakes driven into the bottom permanently mark the places to be periodically monitored. For each assessment, a measuring tape (usually 25 m long) is laid out between the markers, and the macro-organisms within 2 m of the line are quantified.

Visual Assessments

Quantitative observations. Larger organisms within the transect area can be enumerated by simple visual count while swimming along the line. Macroalgae are assessed as to percent cover and relative species abundance.

Supplemental observations. It is important to include the many general, non-quantitative observations that are made during the course of a study--both inside and outside of the study site. General impressions gained from casual observations frequently provide meaningful insight into behavior and distribution of both invertebrates and fishes. Often such insight is needed for meaningful analysis of the quantitative data.

Collecting Procedures

Fishes. For gut content analysis, most fishes are collected by spear, but quinaldine is used to sample the most cryptic forms. The spears are multipronged and vary in length from 2 to 8 feet to meet the differing needs in collecting various sizes and species of fishes.

Algae associates. The organisms associated with the 3 or 4 most dominant species of macroalgae are collected by placing bags (fine mesh or plastic) over the algae and cutting it free. To evaluate substrata preference of the associated organisms an attempt is always made to collect a single species of algae in each bag. Other arborescent forms such as certain hydroids and ectoprocts are collected in the same manner when analyses of their associates are warranted.

Plankton. Organisms occurring in midwater are collected by pushing a meter net through the water column at a specific depth for a specific length of time. This method permits precise measurements of the organisms occurring at specific depths above particular substrata or habitats (see Hobson and Chess, 1976, 1978).

Epifauna. An airlift device, as described earlier (Chess, 1978), is used to quantitatively collect the epifauna from rock bottoms. The procedure described in this report is basically the same but employs a more versatile device (Fig. 1). Organisms are collected from within a $.25 \text{ m}^2$ quadrat, using the airlift like a vacuum cleaner. The organisms are drawn up the tube, through a one-way valve and into a mesh collecting bag.

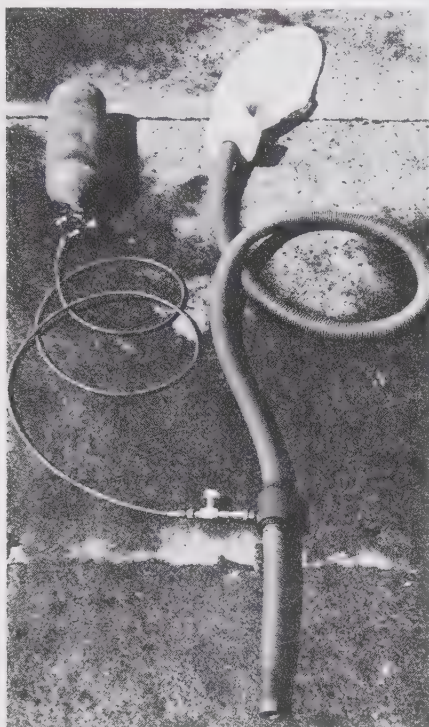


Figure 1. Flexible airlift device.

The modified device is made of flexible plastic corrugated swimming pool cleaner hose (38 mm I.D., 3 m long) rather than rigid PVC pipe. Two advantages of the flexible airlift is portability and ease of use in rough water. It can be easily coiled and stowed in a small boat. In strong wave surge the tube's flexibility allows it to sway back and forth, enabling the operator to maintain position and direct the nozzle of the airlift much easier than with the rigid tube.

As with the earlier device, this airlift is powered by low pressure air from a scuba regulator, either the diver's or a separate unit. Both devices are held vertical in the water by a donut buoy attached to the top and lead weights to the bottom. It is convenient to have the air supply (scuba tank) suspended in the water so that the valve and regulator are not damaged by striking the bottom and to increase mobility of the whole apparatus. Certain small steel or aluminum air tanks are buoyant when only partially filled (about 1500 psi). The manifold used to introduce air into the tube is a

12 cm length of PVC pipe glued top and bottom around a perforated portion of the tube. An even flow of small bubbles from the perforations causes less turbulence and is more efficient than if large bubbles from a single air inlet were employed. The one-way valve at the top of the tube prevents escapement of organisms back down the tube. It can be easily fabricated of wet-suit neoprene by first gluing a piece about 15 cm long into a cylinder of sufficient diameter to slip over the tip of the tube, then cutting two opposite sides from the top about 1/3 down and gluing the margins of the inside edges of the cut together, thereby forming a closed slit at the top. It allows easy flow of air and material into the bag and prevents its return. The collecting bags are fabricated of .333 mm plankton net material.

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Thermoregulation in Tunas

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SYNOPSIS. Because tunas possess countercurrent vascular pathways serving the trunk musculature, metabolic heat is retained, and muscle temperatures can considerably exceed that of the surrounding water (+1° to +21°C). And because tunas have this excess, it is reasonable to suppose they have some means of controlling its magnitude. Tunas must contend with two exigencies which can perturb body temperature: changes in water temperature and, in contrast to non-thermoconserving fish, changes in activity. Both can be met by adaptive change in excess muscle temperature. If this could be accomplished in the absence of changes in environmental temperature or activity level, this would constitute physiological thermoregulation. If excess muscle temperature cannot be altered sufficiently to acceptable levels, more favorable environmental temperatures must be sought or activity levels changed. We would consider this behavioral thermoregulation. High sustained swim speeds, characteristic of the continuously swimming tunas, require special consideration. Heat production is proportional to approximately the cube of swim speed. In order to maintain a slight temperature excess at basal swim speeds (1-2 lengths/sec), and yet not overheat during sustained high speed swimming (>4 lengths/sec), mechanisms are required to conserve heat under the former conditions and to dissipate it effectively under the latter. In this report, we review published observations other investigators have interpreted as physiological thermoregulation in tunas, describe recent findings in our laboratory, and suggest some possible thermoregulatory mechanisms.

INTRODUCTION

Tunas cannot be strictly classified as either poikilotherms or homeotherms. They are "thermoconserving" fish which can maintain muscle temperatures (T_b) several degrees above ambient (T_a). The thermoconserving mechanism, the countercurrent rete in the vascular system serving the trunk musculature (reviewed recently by Stevens and Neill, 1978),

taxonomically distinguishes the 13 species of true tunas (tribe Thunnini) from other members of the family Scombridae, e.g., the bonitos, seerfishes, and mackerels (Klawe, 1977; Collette, 1978). All true tunas have heat exchangers and all get hot (Carey *et al.*, 1971). There are seven species within the genus *Thunnus*, three in *Euthynnus*, two in *Auxis*, and one monotypic genus, *Katsuwonus*. As adults, the *Thunnus* spp. and *Katsuwonus pelamis* are pelagic fish that are distributed more or less continuously across the oceans; the others seldom occur more than a few hundred miles from land (Blackburn, 1965).

Because of the countercurrent rete, metabolic heat is retained and muscle temperatures range from 1° to 21°C above ambient (Barrett and Hester, 1964; Carey *et al.*, 1971; Stevens and Fry, 1971;

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Graham, 1975; Dizon *et al.*, 1978; Stevens and Neill, 1978). Because tunas are fast, continuous swimmers, and are the most highly adapted members of their family for life in the resource-poor pelagic oceans (Magnuson, 1973, 1978), elevated muscle temperatures have been hypothesized to increase muscle power (Carey *et al.*, 1971), maximum swim speed (Graham, 1975), thermal inertia (Neill and Stevens, 1974; Neill *et al.*, 1976), maximum sustained swim speed (George and Stevens, 1978), and muscle efficiency, *i.e.*, getting more kilometers per calorie. Stevens and Neill (1978) have outlined the arguments suggested above.

Aside from the fact of warm-bodiedness, investigators do not agree on why tunas maintain an excess muscle temperature (T_x , where: $T_x = T_b - T_a$) or if they can control T_x in response to thermoregulatory needs. For the purpose of this essay, we will assume that it is of significant benefit to maintain muscle temperatures above ambient. We will, however, establish that 1) control of T_x is demonstrable in at least 2 of the 13 species of tunas, 2) because of the fast sustained swim speeds in tunas, control is theoretically necessary, and 3) physiological control is possible.

THERMOREGULATORY OPTIONS FOR TUNAS

Before proceeding, we wish to clarify how we conceptualize the process of thermoregulation in tunas; we intend it to do no more than facilitate subsequent discussion. We define thermoregulatory options open to tunas as follows:

Behavioral thermoregulation

We subdivide behavioral thermoregulation into two types: a) by environmental selection (Reynolds, 1977), and b) by control of activity-dependent heat production. The first subdivision is open to all fish living in heterothermal environments. We know tunas have sensors to perceive ambient temperature changes (Dizon *et al.*, 1974, 1976; Steffel *et al.*, 1976), and they

are mobile and live in a heterothermal environment. Their ranges, except for bluefin tuna (*Thunnus thynnus*), are narrowly circumscribed by temperature. Bluefin tuna have been observed in waters where surface temperatures range from 6° to 30°C (Carey and Teal, 1969; Sharp, 1978) but commercial concentrations occur between 14° and 21°C (Laevastu and Rosa, 1963). Like bluefin tuna, albacore (*T. alalunga*) are considered a temperate species and are found in fishable concentrations between 16° and 19°C (Laurs and Lynn, 1977). Tropical yellowfin tuna (*T. albacares*) are fished between 23° and 32°C (Sharp, 1978) and skipjack tuna (*Katsuwonus pelamis*), the other so-called tropical tuna, are fished between 19° and 23°C but observed between 17° and 28°C (Laevastu and Rosa, 1963). Little is known about the other less commercially important species. If these data, based on sea-surface temperatures, reflect actual temperature preference, tunas can behaviorally thermoregulate.

Because tunas are thermoconserving fish, they have a behavioral thermoregulatory option not open to other teleosts. They can presumably alter heat production simply by altering their activity levels. Approximately 80% of the free energy liberated by the propulsive musculature appears as heat (Webb, 1975). Heat production is related to approximately the cube of swim velocity (a fundamental relationship; see collected papers in Wu *et al.*, 1975). T_b is a function of heat production and heat dissipation. Alterations of T_b by changes of activity-related heat production would represent the second type of behavioral thermoregulation.

Passive thermoregulation

Here, we include any process that tends to stabilize T_b and which requires no CNS intervention:

a) Water temperature-related and swim velocity-related heat production. Temperature changes affect the viscosity and density of seawater and therefore alter the energetic requirements of a swimming animal (Ware, 1978). Also, as velocity increases, the coefficient of drag decreases

slightly; some energy is saved here (Webb, 1975). Although the effects of temperature, swim speed, viscosity, and density are somewhat compensatory in terms of drag and, thus, heat production, their effects cannot be ignored and must be taken into account in any heat production-dissipation models. Otherwise these effects, in concert with others, could be responsible for observed thermoregulatory ability of tunas.

b) Thermal inertia. Thermal inertia may explain the observed stability of muscle and stomach temperatures in the giant bluefin tuna (Carey *et al.*, 1971; Carey and Lawson, 1973). Because of the countercurrent heat exchangers possessed by tunas, heat is exchanged with the environment at a much reduced rate when compared with other similar-sized teleosts (Neill and Stevens, 1974). Therefore, T_b can lag significantly behind abrupt changes in T_a . Neill and his colleagues (Neill and Stevens, 1974; Neill *et al.*, 1976) have quantified these effects.

c) Swim velocity-related heat dissipation. Under specified circumstances swim speed changes alter surface heat dissipation rate (Tracy, 1972; Erskine and Spotila, 1977; Brill *et al.*, 1978). Increased velocity can cause increased body surface heat loss (mathematical relationship generated for tunas by Sharp and Vlymen, 1978). Later we will discuss whether this increased convective-enhanced surface conductance (Strunk, 1973) could compensate for increased heat production in tunas.

The effectiveness of countercurrent heat exchangers are dependent upon length of the channels, velocity of the fluids within the channels, and the thermal transfer characteristics of the fluids and the channel walls (Mitchell and Myers, 1968). Because the effectiveness of tuna's vascular countercurrent system is inversely related to blood flow, increases in cardiac output, required by increases in swim velocity, could decrease the heat exchanger's effectiveness so that increased heat production could be dissipated without appreciably increasing T_x . Carey and Teal (1969) observed that violent struggles of fish caught on hook and line do indeed reduce, rather than increase, T_b of large bluefin tuna.

Physiological thermoregulation

Here, we wish to be more restrictive in our definition. Activity-independent (*i.e.*, physiological) thermoregulation requires that the CNS has the ability to alter the effectiveness of the thermoconserving mechanisms. Presumably, these changes are mediated by a thermoregulatory center homologous to that in the anterior forebrain of birds and mammals (Crawshaw, 1977; Kluger, 1978). Proof of physiological thermoregulation will be alterations in T_x independent of or opposite to activity-related changes in heat production, when passive thermoregulatory effects are discounted. The remainder of the essay will deal with this topic.

Although our definition of physiological thermoregulation focuses on CNS-mediated changes in heat dissipation, biochemical control of heat production may exist. However, our data only allows us to distinguish behavioral from physiological thermoregulation, not physiological from biochemical. In addition, use of basic hydrodynamic principles allows us to distinguish physiological thermoregulation from what we term passive thermoregulation. Investigation into biochemical solutions by tunas to acute or chronic temperature challenges have yet to be initiated.

FIELD EVIDENCE FOR TUNA THERMOREGULATION

Can field evidence be used to demonstrate thermoregulatory abilities of tuna? If so, what types? Presumably, if T_b 's were relatively constant and independent of T_a , considerable thermoregulatory ability could be assumed (Bligh and Johnson, 1973).

Figure 1 summarizes the existing field observations concerning the abilities of tunas to defend a relatively fixed T_b . Barrett and Hester (1964) determined the following linear least squares regression relationships between muscle temperatures and sea-surface temperatures for skipjack and yellowfin tunas:

$$T_b = .081 T_a + 7.47 \text{ (yellowfin tuna) and} \\ T_b = .58 T_a + 16.39 \text{ (skipjack tuna).}$$

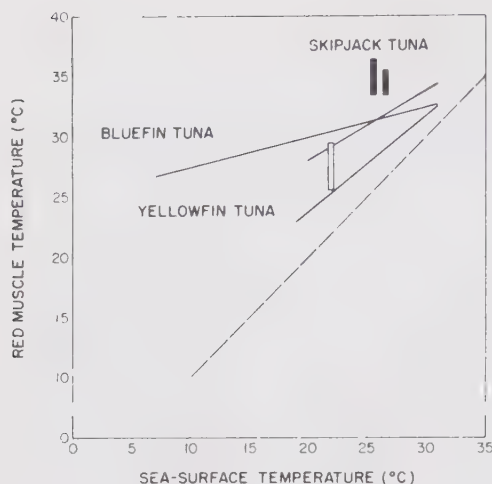


FIG. 1. Linear regression of red muscle temperature (T_b) on sea-surface temperature for skipjack and yellowfin tunas (SJ and YF, respectively, from Barrett and Hester, 1964) and bluefin tuna (BF, from Carey and Teal, 1969). Solid bars are ranges of red muscle temperatures from skipjack tuna (from Stevens and Fry, 1971—right-hand bar from 9 fish averaging 73.5 cm FL, left-hand bar from 20 fish averaging 44.5 cm FL). Open bar is range of red muscle temperatures from skipjack tuna (from Carey and Teal, 1969).

The results were significantly different in slope and level. Over the range tested, size was an unimportant determinant of body temperature in yellowfin tuna. However, larger skipjack tuna tended to be slightly warmer:

$$T_b = 0.59 T_a + 0.015 L + 8.63$$

where L = fork length, mm.

The slopes were significantly different from unity, therefore fish from cooler waters tended to have greater T_x 's, a first indication of a thermoregulatory response.

By the test of "slope," (Fig. 1) bluefin tuna are quite adept at temperature regulation (Carey and Teal, 1969):

$$T_b = 0.25 T_a + 24.94.$$

Bluefin tuna apparently maintain greater independence of T_b from T_a and are also relatively warmer than either skipjack or yellowfin tunas (at least at the center of their ambient temperature range. Their T_b 's varied only 5°C over a range of sea-

surface temperature from 7° to 30°C. The greatest T_x observed was 21.5°C in areas of 7.3°C surface-water temperature.

At least for skipjack tuna, the regression relationship presented by Barrett and Hester (1964) is confounded by additional information from Carey and Teal (1969) and Stevens and Fry (1971). The former observed excess muscle temperatures below (Fig. 1, open bar) and the latter, above (Fig. 1, solid bars) values predicted by Barrett and Hester (1964). The excess red muscle temperatures observed by Stevens and Fry (1971) are almost double those observed by Barrett and Hester (1964) although the fish were taken from areas with the same surface-water temperatures; thus it appears that body temperatures of tunas, at least skipjack, are quite labile.

Nevertheless, as a result of their own and Barrett and Hester's (1964) observations, Carey and Teal (1969) concluded that bluefin tuna were more adept at temperature control than skipjack or yellowfin tunas. Stevens and Fry (1971) concluded that skipjack tuna could also maintain a fixed T_b in waters of 25° to 34°C. Carey and Teal (1969, p. 212) implied that a physiological thermoregulatory mechanism might be employed by the bluefin tuna: "Modifications of the rete under the fish's (bluefin tuna) control maintain temperatures at a constant level." Stevens and Fry (1971) simply state that skipjack tuna regulate muscle temperature; they do not suggest a mechanism.

However, does this field data justify the conclusion that tunas control their muscle temperatures? We do not think so. Evidence from just captured fish is difficult to interpret because:

- 1) The fish have experienced an unknown thermal history. The open ocean is a heterothermal environment. Very cool water is available at depths easily reached by tunas because all but the largest species lack swim bladders, or have swim bladders which are reduced in size or atrophied (Godsil and Byers, 1944; Gibbs and Collette, 1971). Dizon *et al.* (1978) show that extensive vertical migrations (surface to 273 m) are continuous features of the day-

light activity pattern of skipjack tuna (70 cm), in areas where T_a ranged from 25°C at the surface to less than 12°C at 270 m depth. Because all tunas possess a degree of thermal inertia, their characteristic T_b would be a function of the sequence of ambient temperatures experienced prior to capture, and not just the sea-surface temperature used by Barrett and Hester (1964), Carey and Teal (1969), and Stevens and Fry (1971). Looking for thermoregulatory ability by relating T_b to T_a is meaningful only if T_a has been constant long enough for the fish to reach thermal steady state (Neill and Stevens 1974; Neill *et al.*, 1976). This time period is size-related, and is thus especially important for larger tuna.

2) As described earlier, there is a fundamental relationship between activity and heat production, but field evidence is contradictory on the effect of activity on T_b . Carey and Teal (1966) show that "lively" bigeye tuna (*Thunnus obesus*) have higher body temperatures than "weak" ones. Also, Stevens and Fry (1971) unequivocally demonstrate that skipjack tuna T_x 's increase by one-third when strenuously exercised, but Carey and Teal (1969) show that hook-and-line caught fish have lower muscle temperatures than trap-caught ones. Even though hook-and-line fish presumably have fought harder and longer than trap-caught fish, they are cooler.

3) Perhaps, fish measured at different surface-water temperatures, in widely divergent geographical areas, are members of different stocks (Sharp, 1978). T_x differences might result from acclimation processes spanning days to generations (Hazel and Prosser, 1974).

To alleviate uncertainties outlined above, Carey and Lawson (1973) proposed an experiment involving long-term monitoring of T_b in response to controlled changes in T_a . They designed a field experiment using the naturally occurring heterothermal conditions around Nova Scotia, the northernmost range of giant bluefin tuna. Ultrasonic transmitters were used to simultaneously monitor stomach or muscle temperature and water temperature. (Heat exchangers also service the visceral structures of the more phylogeneti-

cally advanced bluefin tuna group, *cf.*, Kishinouye, 1923; Godsil and Byers, 1944; Gibbs and Collette, 1967.)

Transmitters were placed on 14 bluefin tuna. Because several fish exhibited muscle and stomach temperatures that were independent of T_a 's, Carey and Lawson (1973) concluded that bluefin tuna can thermoregulate in the mammalian sense (*i.e.*, maintain relatively constant body temperatures even though subjected to prolonged changes in T_a) by altering the effectiveness of their vascular heat exchange system.

There is, however, an alternate explanation. Using a purely empirical approach, Neill and Stevens (1974) successfully mathematically modeled the bluefin tuna telemetry data assuming a constant rate of heat dissipation and heat production (Fig. 2). No physiological thermoregulatory mechanisms dependent upon T_a were postulated, and yet the model could explain the observed muscle and stomach temperature stability observed by Carey and Lawson (1973).

Although the Neill and Stevens' (1974) analysis does not prove or disprove the possibility that bluefin tuna are capable of rapid physiological thermoregulation, thermal inertia (passive thermoregulation) of these large tunas may well have accounted for the observed stability of T_b .

LABORATORY EVIDENCE FOR TUNA THERMOREGULATION

To differentiate between behavioral, passive, or physiological thermoregulation requires an experiment that monitors activity levels at constant T_a for long periods of time. We designed equipment to control T_a precisely in a tank sufficiently large to accommodate small yellowfin and skipjack tunas, which are routinely maintained in captivity at the Kewalo Research Facility in Honolulu (Nakamura, 1972). To monitor muscle temperature, we employed a small, ultrasonic transmitter (Fig. 3; Rochelle and Coutant, 1974). A photocell system monitored activity, and T_a was generally maintained within 0.05°C in the annular-shaped test tank (6.1 m major diam × 5.3 m minor diam × 0.6 m deep, Fig. 3).

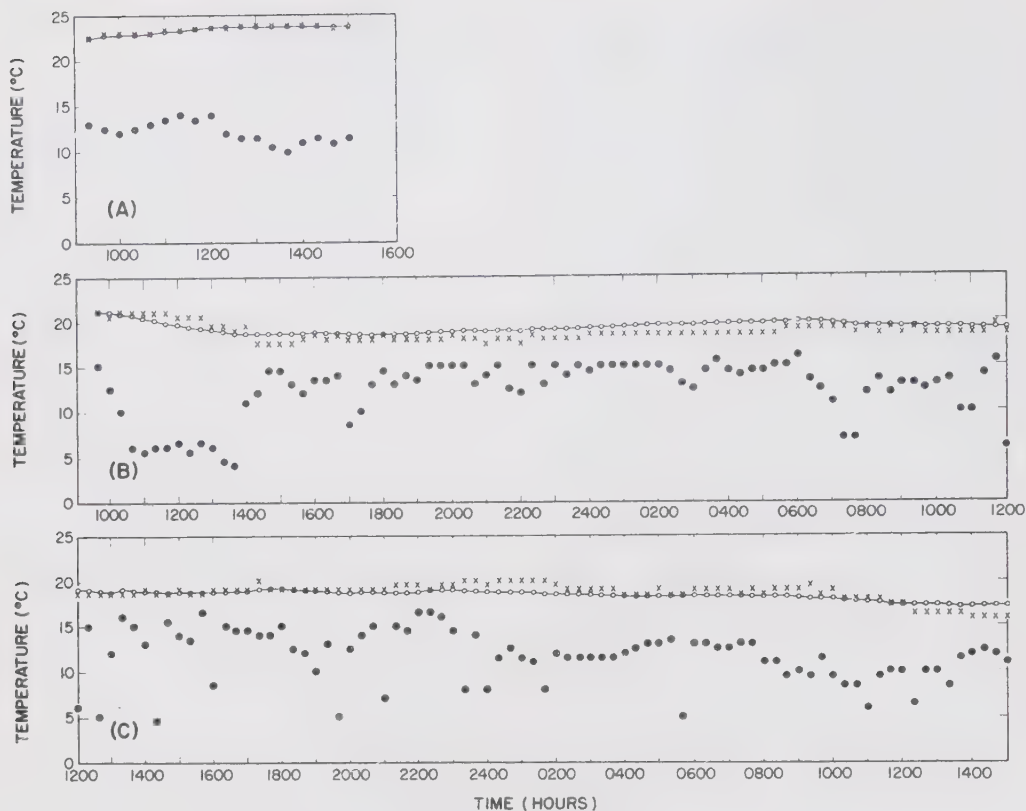


FIG. 2. Actual T_b (x) and modeled T_b (o) of two free-swimming bluefin tuna (Carey and Lawson, 1973) encountering abrupt changes in T_a (•) (from Neill and Stevens, 1974). No assumption of physio-

logical thermoregulation is used in constructing the model, yet the fit is remarkably good. Panel A shows muscle temperatures from bluefin tuna No. 8, B and C show temperatures from bluefin tuna No. 14.

Nine skipjack tuna (SJ 1-9) were individually subjected to consecutive temperature treatments: 4-8 hr at 25°C, 12 hr at 20°C, 12 hr at 30°C, 12 hr at 20°C, and 12 hr at 25°C (Table 1). Six yellowfin tuna (YF 1-6) were subjected to consecutive 12-hr temperature treatments: 25°, 20°, 30°C, 20°C, and 25°C (Table 2). Six other yellowfin tuna (YF 6-12) were subjected to an altered sequence of 12-hr temperature treatments: 25°, 30°, and 25°C (Table 2). To eliminate any effects of thermal inertia, we analyzed only data collected after T_b stabilized following ambient temperature changes. Some sets of data are incomplete because the fish died prematurely or because it would not swim complete laps which are required for the logic equipment to translate position information from the

photocells into swim speed.

Does a simple plot of T_b versus T_a reveal if yellowfin and skipjack tunas are compensating for increasing T_a by reducing T_x , as bluefin tuna seem to do (Carey and Teal, 1969; Carey *et al.*, 1971)? That is, are the slopes of the regression of T_b on T_a significantly different from one? No such compensations occurred (Fig. 4); T_x was independent of T_a . The regression relationships are:

$$T_b = 2.12 + 0.95 T_a \text{ (yellowfin tuna)}$$

$$T_b = 3.14 + 0.97 T_a \text{ (skipjack tuna)}$$

T_b is clearly highly dependent on T_a and skipjack tuna are warmer than yellowfin tuna. At 25°C, the fish in our experiments are 1.5°C cooler than those measured by Barrett and Hester (1964) (27.7°C com-

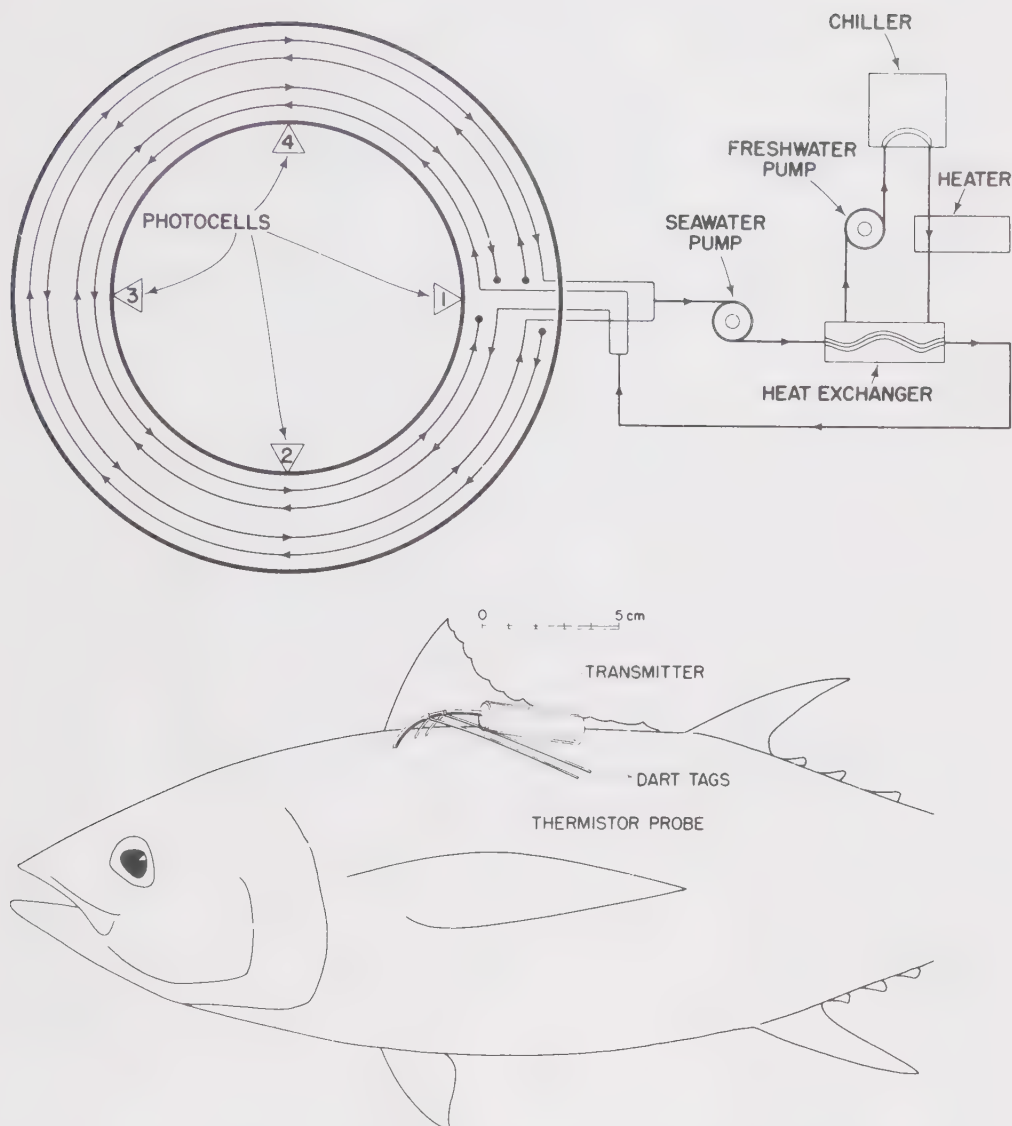


FIG. 3. Schematic diagram of the annular test tank system and of deployment of temperature-sensitive ultrasonic transmitter on a yellowfin tuna. Seawater is

delivered to and removed from the swim channel through countercurrent perforated pipes, so that longitudinal temperature gradients do not develop.

pared to 26.2°C for the yellowfin tuna and 30.9°C compared to 27.2°C for skipjack tuna), probably reflecting the higher states of activity prior to capture of the wild fish. The differences in slope (0.98 *vs.* 0.81 and 0.95 *vs.* 0.58, respectively) are perhaps due either to the unknown past thermal and activity histories, or to long-

term acclimatory adjustments of the fish caught by Barrett and Hester (1964).

The T_x of skipjack tuna exceed those of yellowfin tuna (Tables 1 and 2), but we do not know whether this is due to activity differences or heat exchanger efficiency differences. To resolve this, heat production (Fig. 5, estimated by the following proce-

TABLE 1. Grand mean swim speeds and T_{re} ($\pm 95\%$ confidence limits) for skipjack tuna.^a

	Fork length (cm)	Weight (g)	Test temperatures (°C)				
			25°	20°	30°	20°	25°
<i>Skipjack tuna 1</i>							
Swim speed (cm/sec)	43.3	1,343	77.82 $\pm$ 4.77	64.31 $\pm$ 1.24	93.09 $\pm$ 2.22	—	—
Temperature excess (°C)			3.11 $\pm$ 0.14	3.06 $\pm$ 0.06	3.59 $\pm$ 0.08	—	—
Estimated heat production (watts)			3.02	2.60	3.59	—	—
<i>Skipjack tuna 2</i>							
Swim speed (cm/sec)	46.5	1,673	75.29 $\pm$ 1.62	68.06 $\pm$ 0.55	76.54 $\pm$ 1.71	67.60 $\pm$ 3.35	—
Temperature excess (°C)			2.44 $\pm$ 0.25	2.02 $\pm$ 0.04	1.62 $\pm$ 0.07	2.60 $\pm$ 0.10	—
Estimated heat production (watts)			3.29	3.07	3.26	3.05	—
<i>Skipjack tuna 3</i>							
Swim speed (cm/sec)	46.1	1,758	61.47 $\pm$ 0.99	44.24 $\pm$ 1.77	62.43 $\pm$ 0.86	62.97 $\pm$ 2.98	72.16 $\pm$ 0.68
Temperature excess (°C)			1.97 $\pm$ 0.10	3.13 $\pm$ 0.07	1.71 $\pm$ 0.02	2.40 $\pm$ 0.14	1.86 $\pm$ 0.09
Estimated heat production (watts)			2.84	2.45	2.82	2.93	3.21
<i>Skipjack tuna 4</i>							
Swim speed (cm/sec)	46.3	1,826	75.70 $\pm$ 1.01	68.43 $\pm$ 0.73	75.91 $\pm$ 1.80	—	68.60 $\pm$ 1.19
Temperature excess (°C)			1.37 $\pm$ 0.10	1.17 $\pm$ 0.03	1.44 $\pm$ 0.04	—	1.47 $\pm$ 0.04
Estimated heat production (watts)			3.40	3.18	3.33	—	3.13
<i>Skipjack tuna 5</i>							
Swim speed (cm/sec)	47.6	1,918	67.76 $\pm$ 1.04	68.43 $\pm$ 1.09	81.48 $\pm$ 0.99	68.94 $\pm$ 1.10	72.54 $\pm$ 1.41
Temperature excess (°C)			1.27 $\pm$ 0.03	1.30 $\pm$ 0.03	1.52 $\pm$ 0.08	1.55 $\pm$ 0.03	1.55 $\pm$ 0.04
Estimated heat production (watts)			3.20	3.28	3.68	3.30	3.38
<i>Skipjack tuna 6</i>							
Swim speed (cm/sec)	43.4	1,154	79.84 $\pm$ 3.54	74.85 $\pm$ 2.38	—	—	—
Temperature excess (°C)			1.84 $\pm$ 0.16	3.31 $\pm$ 0.09	—	—	—
Estimated heat production (watts)			2.96	2.83	—	—	—
<i>Skipjack tuna 7</i>							
Swim speed (cm/sec)	48.6	1,708	87.37 $\pm$ 2.45	77.82 $\pm$ 0.61	75.51 $\pm$ 1.36	60.79 $\pm$ 3.75	—
Temperature excess (°C)			1.77 $\pm$ 0.08	1.45 $\pm$ 0.01	2.26 $\pm$ 0.14	2.83 $\pm$ 0.17	—
Estimated heat production (watts)			4.00	3.60	3.33	2.89	—
<i>Skipjack tuna 8</i>							
Swim speed (cm/sec)	47.9	1,640	61.83 $\pm$ 1.54	57.82 $\pm$ 3.05	—	—	—
Temperature excess (°C)			1.98 $\pm$ 0.04	1.68 $\pm$ 0.09	—	—	—
Estimated heat production (watts)			2.82	2.73	—	—	—
<i>Skipjack tuna 9</i>							
Swim speed (cm/sec)	45.4	1,405	59.11 $\pm$ 1.20	58.61 $\pm$ 0.51	63.08 $\pm$ 1.17	54.08 $\pm$ 0.57	—
Temperature excess (°C)			3.81 $\pm$ 0.08	3.61 $\pm$ 0.07	2.90 $\pm$ 0.08	2.93 $\pm$ 0.10	—
Estimated heat production (watts)			2.51	2.53	2.58	2.41	—

^a Heat production is based on swim speed, muscle efficiency, and standard metabolic rate.^b SJ 4 and 5 had the thermistor probe in their white muscle.

TABLE 2. Grand mean swim speeds and T_{re} 's ($\pm 95\%$ confidence limits) for yellowfin tuna.^a

	Fork length (cm)	Weight (g)	Test temperatures (°C)			
			25°	20°	30°	25°
<i>Yellowfin tuna 1</i>	45.9	1,853				
Swim speed (cm/sec)			55.00 $\pm$ 1.06	45.55 $\pm$ 0.36	65.61 $\pm$ 1.30	50.47 $\pm$ 1.34
Temperature excess (°C)			1.34 $\pm$ 0.03	1.07 $\pm$ 0.02	0.94 $\pm$ 0.01	1.24 $\pm$ 0.06
Estimated heat production (watts)			2.72	2.53	2.98	2.61
<i>Yellowfin tuna 2</i>	47.8	2,219				
Swim speed (cm/sec)			67.88 $\pm$ 1.56	67.34 $\pm$ 1.27	84.82 $\pm$ 2.56	73.70 $\pm$ 1.37
Temperature excess (°C)			1.47 $\pm$ 0.02	1.28 $\pm$ 0.03	0.62 $\pm$ 0.01	1.48 $\pm$ 0.03
Estimated heat production (watts)			3.40	3.43	4.04	3.63
<i>Yellowfin tuna 3</i>	45.5	2,677				
Swim speed (cm/sec)			51.70 $\pm$ 1.32	51.13 $\pm$ 0.28	77.48 $\pm$ 1.65	55.10 $\pm$ 1.48
Temperature excess (°C)			1.30 $\pm$ 0.09	1.38 $\pm$ 0.01	1.05 $\pm$ 0.04	1.42 $\pm$ 0.04
Estimated heat production (watts)			3.13	3.15	3.88	3.21
<i>Yellowfin tuna 4</i>	48.3	1,942				
Swim speed (cm/sec)			55.67 $\pm$ 0.89	46.54 $\pm$ 1.28	57.91 $\pm$ 2.72	—
Temperature excess (°C)			1.75 $\pm$ 0.05	1.43 $\pm$ 0.04	0.90 $\pm$ 0.02	—
Estimated heat production (watts)			2.84	2.64	2.86	—
<i>Yellowfin tuna 5</i>	66.4	6,035				
Swim speed (cm/sec)			52.38 $\pm$ 1.54	51.17 $\pm$ 0.96	66.89 $\pm$ 1.55	57.79 $\pm$ 2.41
Temperature excess (°C)			1.72 $\pm$ 0.06	1.87 $\pm$ 0.05	0.63 $\pm$ 0.02	1.85 $\pm$ 0.10
Estimated heat production (watts)			5.07	5.07	5.70	5.30
<i>Yellowfin tuna 6</i>	45.0	1,491				
Swim speed (cm/sec)			67.52 $\pm$ 0.61	47.88 $\pm$ 1.81	61.52 $\pm$ 1.07	49.72 $\pm$ 1.02
Temperature excess (°C)			0.99 $\pm$ 0.13	0.27 $\pm$ 0.06	0.64 $\pm$ 0.02	0.76 $\pm$ 0.01
Estimated heat production (watts)			2.82	2.32	2.59	2.34
Test temperatures (°C)						
			25°	30°	20°	25°
<i>Yellowfin tuna 7</i>	54.5	2,784				
Swim speed (cm/sec)			67.08 $\pm$ 1.27	62.70 $\pm$ 0.77	43.16 $\pm$ 0.34	58.35 $\pm$ 1.38
Temperature excess (°C)			0.64 $\pm$ 0.09	0.54 $\pm$ 0.02	0.51 $\pm$ 0.03	0.74 $\pm$ 0.02
Estimated heat production (watts)			3.91	3.66	3.14	3.56
<i>Yellowfin tuna 8</i>	65.0	3,797				
Swim speed (cm/sec)			42.83 $\pm$ 0.55	83.39 $\pm$ 4.13	—	—
Temperature excess (°C)			0.81 $\pm$ 0.02	0.66 $\pm$ 0.04	—	—
Estimated heat production (watts)			3.74	5.74	—	—

^a Heat production is based on swim speed, muscle efficiency, and standard metabolic rate.

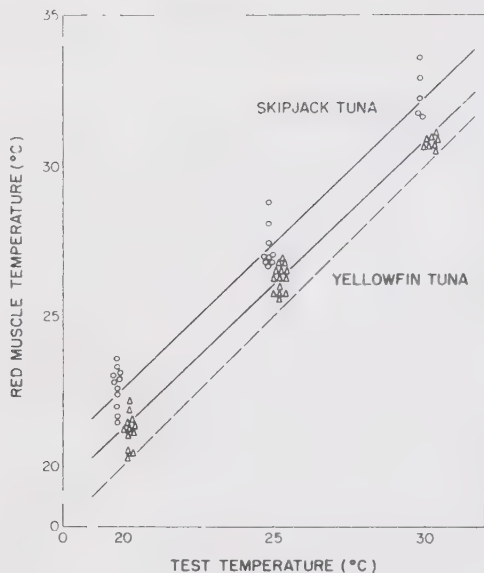


FIG. 4. Linear regression of red muscle temperature (T_b) on ambient temperature (T_a). Relationships are: $T_b = 2.12 + 0.95 T_a$ (yellowfin tuna) and $T_b = 3.14 + 0.97 T_a$ (skipjack tuna). The dotted line is $T_b = T_a$.

dures, see also Webb, 1975; Sharp and Francis, 1976; Sharp and Vlymen, 1978; Ware, 1978; and Wu and Yates, 1978) was used as a covariate because it accounts for swim velocity, fish size, and the temperature-dependent properties (viscosity and density) of seawater.

$$P_1 = (0.5 \cdot \rho \cdot V^3 \cdot S \cdot C_d \cdot 10^7) \cdot \eta^{-1} \quad (1)$$

where

P_1 = input metabolic power to the swimming muscles (watts)

η = muscle efficiency, in this instance the efficiency of converting chemical energy into propulsive power (dimensionless), ~ 0.2 (Brown and Muir, 1970; Webb, 1975). Note, the caudal fin is assumed to be 100% efficient;

ρ = seawater density (g/cm³) a temperature-dependent parameter;

V = swim velocity (cm/sec);

S = surface area, which is approximately equal to $0.4 L^2$ where L is fork length in centimeters (Webb, 1975);

C_d = drag coefficient (dimensionless), a temperature, velocity, and length dependent empirical constant equal to:

$$C_d \approx 10 R_L^{-0.5} \quad (2)$$

where

$$R_L = \rho \cdot V \cdot L \cdot \mu^{-1} \quad (3)$$

R_L = Reynolds number

μ = seawater viscosity (poise), a temperature-dependent property.

Brill (1979) estimated standard metabolic rate (SMR) for skipjack tuna as:

$$P_2 = 1.53 W^{0.563}, \quad (4)$$

where

P_2 = SMR (watts),

W = weight (Kg).

We hope this is similar for yellowfin tuna.

Heat production within the muscle of the fish is assumed to be approximately equal to P_1 (the input metabolic power)

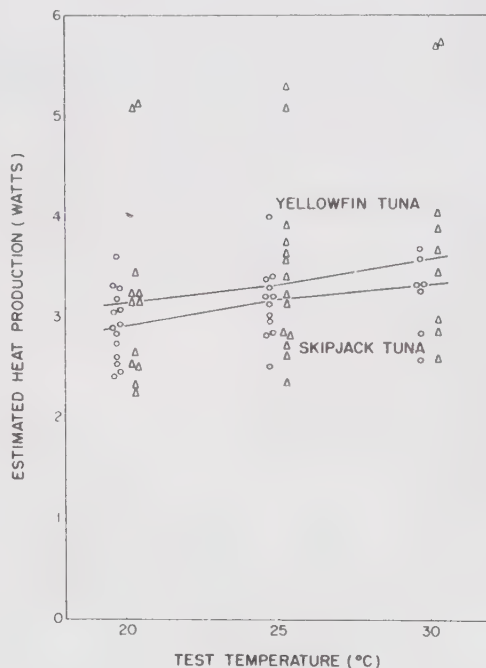


FIG. 5. Estimated heat production (based on swim speed, muscle efficiency, and standard metabolic rate) at each test temperature. The lines are drawn through the median heat production estimates. $\circ$ —skipjack tuna, Δ —yellowfin tuna.

minus the output power dissipated as thrust, plus P_2 (the SMR),

$$H_p = (1 - \eta) P_1 + P_2 \quad (5)$$

It thus appears (Fig. 5), that although the T_x values of skipjack tuna are above those of yellowfin tuna, heat production in yellowfin tuna is generally higher. For both fish, heat production increases with T_a .

Yet, here we have a contradiction. Figure 4 indicates no thermoregulatory ability, T_x remains virtually constant over the 10° range of test temperatures. Because heat production also increases at 30°C (especially in yellowfin tuna, Fig. 5), heat dissipation rate per degree of driving gradient must be greater at higher test temperatures. The ability to maintain a constant T_x at various levels of heat production suggests that heat dissipation per degree of driving gradient is variable, and possibly controllable.

Mammalian physiologists (Kleiber, 1972) often employ an index of whole-body thermal conductance to quantify thermoregulatory ability:

$$H_L = K \cdot (T_b - T_a), \quad (6)$$

where

H_L = steady state heat loss (T_b is not changing, therefore $H_L = H_p$) (watts), and

K = whole body thermal conductance (watts/°C).

Whole body thermal conductance (K) includes thermal conditions within the animal and the environment (Tracy, 1972). Comparisons will be made only between temperature treatments, not fish; we are concerned only with how K changes with T_a and not its absolute value. For this reason, absolute values of heat production are less important and the use of K is justified.

Yellowfin tuna seem the most adept at thermal regulation (Fig. 6). YF 1-5 and YF 8 seem to have controlled their heat dissipation rate appropriately; K was greatest at 30°C (close to upper preferred ambient temperature, 32°C, Sharp, 1978), reduced at 25°C, and reduced still further at 20°C in some fish. YF 6 and 7 show no apparent pattern, T_a and K were uncorrelated.

In contrast to yellowfin tuna, skipjack tuna exhibited great variability in whole body thermal conductance over the three test temperatures (Fig. 6). SJ 1, 2, 5, and 9 showed a significant increase in K during the 30°C test treatment. For the other fish, large changes in K were the only commonality. In some cases, the alteration in T_x was appropriate, decreasing in the face of increasing T_a and the heat load imposed by faster swimming; in other cases it was not. However, the significance of these data are that alterations in swim speed, and consequently, heat production were not accompanied by expected changes in T_x (Tables 1 and 2), even though heat production is inexorably linked to swim speed. Clearly, some mechanism intervenes to alter the pattern of heat loss, heat generation, or both.

In our experiment, the changes in K were appropriate for thermoregulation in six of the eight yellowfin tuna but in only a few of the skipjack tuna. Exceptions were not unexpected, because we are dealing with very small temperature changes within the thermal zones of tolerance for both species. We have also stressed these fish by confinement, and by application of the telemetry device. Under these conditions, appropriate thermoregulatory responses may have been impossible for some of the fish, or simply not necessary.

When a tuna is forced to swim at greater speeds (and hence has higher internal heat production) in water temperatures close to its upper lethal temperature, thermoregulation is more critical. We increased swim speed in 23 skipjack tuna by increasing their density which demands faster swimming in order to maintain hydrostatic equilibrium. These fish have no swim bladder. Only three survived long enough to give meaningful data after force-feeding the plastic-coated weights and attaching the ultrasonic transmitter. Data were collected for 12 hr at 25°C and subsequently 12 hr at 30°C (Table 3). SJ 1 responded to the increase in ambient temperature by reducing both swim speed and muscle temperature (Table 3), perhaps a behavioral thermoregulatory response. Because of the weights, SJ 2 and 3 apparently could

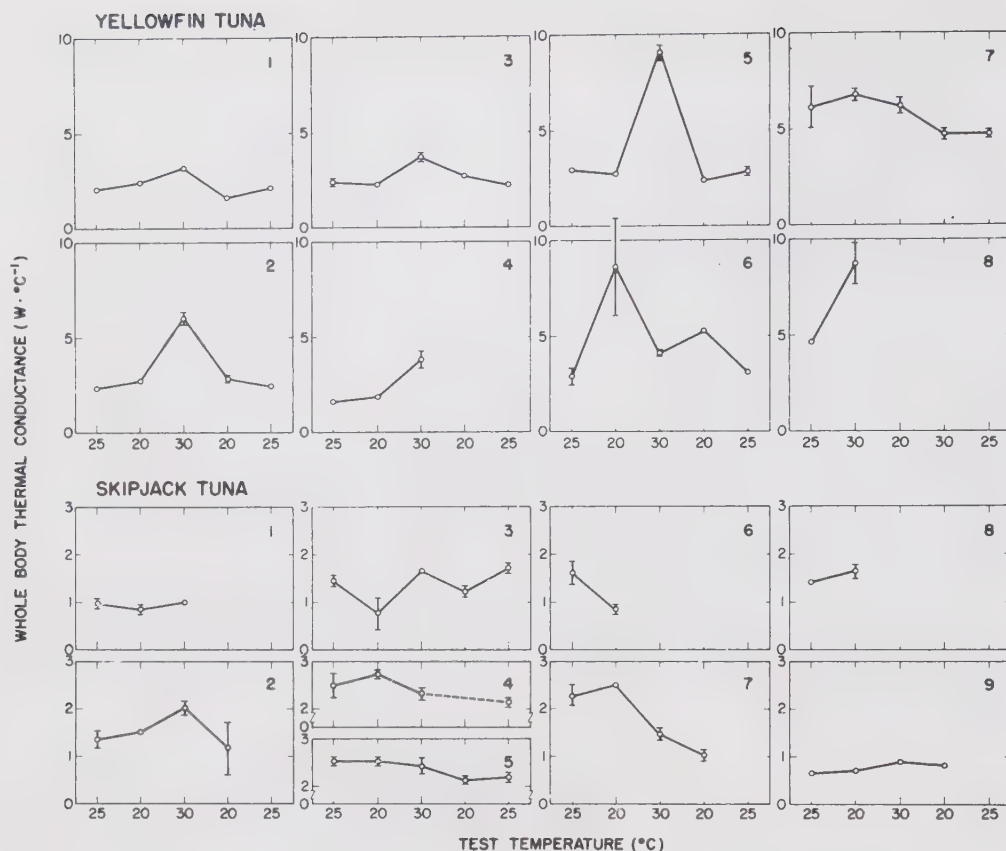


FIG. 6. The effect of ambient temperature on whole body thermal conductance (K). K was determined by dividing estimated heat production by excess muscle temperature (T_x). Vertical lines represent extreme

values of K based upon the 95% confidence limits of mean swim speed and T_x . Note: The K values for SJ 4 and 5 are based upon T_x of white muscle.

not reduce speed significantly, but T_x decreased nonetheless. Mean T_x for SJ 3 at $30^\circ C$ was 40% less than at $25^\circ C$, and we estimated that heat dissipation rate increased 38%. This occurred with no change in swim velocity.

POSSIBLE THERMOREGULATORY MECHANISMS

Our data show that T_x can change directly, inversely, or independently of swim velocity and heat production (Tables 1, 2, and 3), consequently whole body thermal conductance (K) changes quite dramatically (Fig. 6). In addition, yellowfin tuna and weighted skipjack tuna seem to alter their whole body thermal conductance in

an appropriate manner to reduce T_x at high ambient temperatures. But is a conclusion of physiological thermoregulation appropriate? As suggested in the introduction, several processes could serve to stabilize or alter T_x when a fish is confronted with changes in T_a or increased metabolic heat production.

As swim speed increases, increased heat production may be dissipated at a lower T_x because increased blood flow through the countercurrent heat exchangers may reduce their effectiveness (Mitchell and Myers, 1968), thus allowing more heat to be dissipated via the gills. In addition, increased heat production may be more effectively dissipated at the body surface due

TABLE 3. Grand mean swim speeds and T_x 's (95% confidence limits) for skipjack tuna weighted with plastic-coated lead to increase swim speed.

	Fork length (cm)	Weight (g)	Weight carried (g)	Test temperatures (C)	
				25°	30°
<i>Skipjack tuna 1</i>	42.4	1,262	67.5		
Swim speed (cm/sec)				93.82±1.31	89.18±1.10
Temperature excess (°C)				2.79±0.05	2.58±0.04
Estimated heat production (watts)				3.62	3.30
K (watts/°C)				1.30±0.05	1.28±0.07
<i>Skipjack tuna 2</i>	44.7	1,405	86.7		
Swim speed (cm/sec)				87.05±1.50	84.44±1.81
Temperature excess (°C)				3.15±0.06	2.28±0.08
Estimated heat production (watts)				3.54	3.20
K (watts/°C)				1.12±0.05	1.46±0.08
<i>Skipjack tuna 3</i>	41.6	1,174	211.5		
Swim speed (cm/sec)				96.27±1.21	95.88±0.83
Temperature excess (°C)				4.96±0.21	2.95±0.05
Estimated heat production (watts)				3.62	3.48
K (watts/°C)				0.73±0.05	1.18±0.03

to enhancement of surface conduction due to faster water velocity over the body (Tracy, 1972; Strunk, 1973; Erskine and Spotila, 1977; and Brill *et al.*, 1978). Both processes must occur, but they cannot be the sole explanation for our data because we show T_x and swim speed bear no fixed relationship.

Furthermore, the effectiveness of the heat conservation system must drastically decrease with increasing swim speed. A significant T_x is generated at slow speeds but the subsequent cubic increases in heat production are effectively dissipated at reasonable temperature driving gradients. Enhanced surface conduction due to water velocity increases will not compensate for the increased heat production caused by faster swimming. If no physiological thermoregulatory mechanisms are assumed to be operating, T_x will rise approximately as the square of swim speed, since heat production rate is roughly proportional to $V^{2.5}$ and surface conduction is proportional to $V^{0.5}$ (Sharp and Vlymen, 1978). Figure 7 is the T_x velocity relationships of a hypothetical, non-thermoregulating yellowfin tuna (the same size as YF 5); the independent variable in this mathematical model (created by Sharp and Vlymen, 1978) is swim speed, no changes in internal thermal conductivity or gill heat loss are assumed. In the absence of any effective ther-

moregulatory mechanisms, T_x obtains absurd levels at the sustainable speed of 4 lengths/sec, even if the heat exchanger is only 25% efficient (*i.e.*, 75% of the estimated heat production is dissipated via the gills). Clearly, in a real tuna, some mechanism must intervene to increase thermal conductivity as swim speed increases, and this mechanism must have a greater dynamic range than convective-enhanced surface conduction or the reduction in effectiveness of the heat exchanger due to faster blood flow through its vessels. For these reasons and the lack of any predictable relationship between swim speed and body temperature, we feel tunas are capable of some degree of physiological thermoregulation.

There are two situations arising for tunas in which changes in heat dissipation rate per degree of driving gradient would be beneficial; 1) T_x may be increased or decreased when ambient temperatures approach lethal limits and 2) increased heat production, brought on by fast swimming, must be effectively dissipated to prevent generation of lethal muscle temperatures. We hypothesize that these two exigencies may be met by physiological processes involving changes in circulatory patterns that alter the effectiveness of the heat exchangers or changes in the relative contributions of the red and white muscle

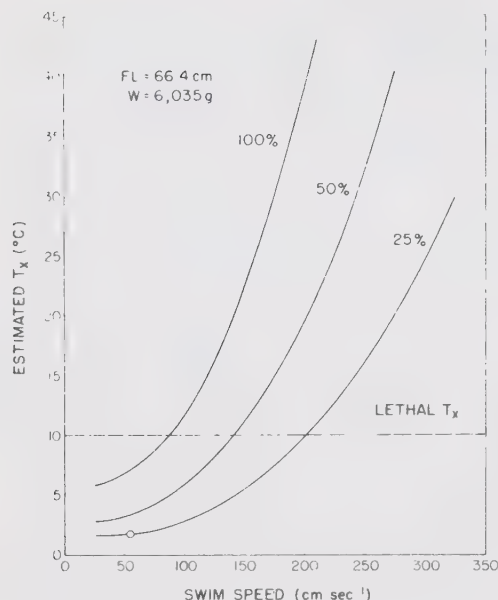


FIG. 7. Predicted excess red muscle temperature (T_x) of a nonthermoregulating tuna similar in size to YF 5 (66.4 cm FL, 6,035 g body weight) as a function of swim speed. Calculation of T_x is based on a model of convective-enhanced surface conductance (Sharp and Vlymen, 1978). The 100% function requires that all metabolic heat be dissipated at the body surface; the other two functions assume 50% and 25% of the estimated heat production is dissipated through the body surface. The latter presumably represent situations where the heat exchangers allow a greater proportion of metabolic heat to be dissipated via the gills. The open dot is the measured mean swim speed and mean T_x of YF 5 at 25°.

fiber systems to propulsion.

The second exigency, prevention of overheating, presents no conceptual problem. However, the notion that white muscle fibers are only used at high, unsustainable swim speeds (only used anaerobically) must be discarded. White muscle fibers of skipjack tuna have the enzymatic capacity to function aerobically (Hochachka *et al.*, 1978), and become active at velocities below maximum sustainable swim speed (Brill and Dizon, unpublished data). Other fish have been shown to use their white muscle fibers at sustainable speeds (Pritchard *et al.*, 1971; Bone, 1975; Bone *et al.*, 1978). White muscle fibers of tunas are supplied by circulatory pathways that bypass the vascular heat exchangers

(Kishinouye, 1923; Godsil and Byers, 1944), therefore heat generated aerobically by this muscle is not retained but dissipated in the same manner as nonthermoconserving fish, via the gills and body surface (Stevens and Sutterlin, 1976; Erskine and Spotila, 1977). We suspect that the contribution of red muscle fibers to propulsion may be limited to slow swim speeds.

Control of the relative contribution of the red and white muscle fibers to propulsion may also serve in fine control of T_x in response to changing T_a . At high ambient temperatures white muscle, which contributes significantly less to the temperature burden of the fish, may be used to a greater extent than red. Alternatively, circulatory modifications within the heat exchangers may alter their effectiveness as thermal barriers. In fish, changes in water temperature and activity significantly affect cardiovascular dynamics by altering the concentrations of circulating catecholamines (Randall, 1970; Stevens *et al.*, 1972; Watters and Smith, 1973). Stevens *et al.* (1974) show that the arterial vessels of the central heat exchanger have thick muscular walls, although apparently not innervated. However, circulating catecholamines could modify circulatory patterns within the central and lateral heat exchangers and thereby alter their effectiveness.

The latter mechanism may be more important in skipjack and yellowfin tunas, because the lateral cutaneous vessels, which supply blood to the white muscle and bypass the heat exchangers, are much smaller than the dorsal aorta and postcardinal vein (Godsil and Byers, 1944), although the cutaneous vessels may be highly distensible. In the other *Thunnus* spp., these vessels are well developed.

SUMMARY

Tunas are thermoconserving fish that sometimes adjust their T_x in an appropriate manner—lower in warm waters, higher in cool. Yet, investigators do not agree whether tunas can regulate T_x , or even the biological advantage of having a T_x . Three thermoregulatory options are theoretically

open to tunas: 1) Behavioral thermoregulation, 2) passive thermoregulation, and 3) physiological thermoregulation, in which heat dissipation rates per degree of driving gradient can be controlled.

Maximum muscle temperatures of recently landed skipjack and yellowfin tunas suggested that as T_a increased, T_b slightly decreased. Is this physiological temperature regulation or the result of interaction of the effects of thermal inertia and past temperature and activity history?

Telemetry measurements from large, free-swimming bluefin tuna have been used to build a case for rapid physiological thermoregulation; subsequent analysis of the same data demonstrated that the thermal inertia characteristic (passive thermoregulation) of tunas is sufficient to explain the observed temperature constancy.

To differentiate between the three forms of thermoregulation, we devised an experiment to monitor T_b and swim speed and maintain T_a for a time sufficiently long so that only steady state T_b 's were used for analysis. Yellowfin and skipjack tunas demonstrated alterations in swim speed that were *not* accompanied by expected changes in T_x . Clearly, skipjack and yellowfin tunas are not prisoners of their own thermoconserving mechanisms. Most of the yellowfin tuna and about half of the skipjack tuna showed appropriate thermal conductance changes (K)—conductance rates rose with increasing T_a . Skipjack tuna forced to swim fast at temperatures close to their upper lethal temperature, were able to reduce T_x without reducing swim speed. Significant is the lack of any predictable relationship because here is where thermoregulatory control may be exerted.

To maintain a significant T_x at slow swim speeds, and yet not overheat during bouts of sustainable high speed swimming requires tuna be able to control heat dissipation. Altering the proportion of red and white muscle power to the caudal propeller might serve the above function. White muscle does not add to the temperature burden because its circulation has no heat exchangers. For basal rate swimming, sufficient temperature excess may be built up through red muscle supplying the

necessary power. As speeds increase, temperature could be kept within acceptable limits by proportionally grading more white muscle fibers into activity. White muscle has been shown to have significant aerobic capacity and to become active at sustainable swim speeds. In addition, circulatory pattern alterations within the heat exchangers may serve to reduce their effectiveness or to shunt proportionally more blood around the heat exchangers.

Thus, tunas have the capacity to control T_b 's by behavioral means, such as seeking more favorable environments or altering swim speeds to change heat production. In addition, passive thermoregulation is possible due to significant thermal inertia. Thermal sequestering of the muscle by the vascular heat exchangers allows tunas to develop a significant T_x and to maintain a temperature constancy extending from minutes to several hours depending upon size. Physiological thermoregulatory mechanisms seem indicated because of the labile and independent nature of T_x and accommodation of very high heat production during fast sustainable swim speeds. These adaptations, as well as acclimatory processes, provide tunas with potent thermoregulatory mechanisms for dealing with their thermally heterogeneous habitats.

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THERMOREGULATION IN YELLOWFIN TUNA, THUNNUS ALBACARES¹

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To determine their capacity for thermoregulation, yellowfin tuna, *Thunnus albacares*, were subjected to a series of 12-h periods at T_a 's of 20, 25, and 30 C. Muscle temperature, measured with an ultrasonic transmitter attached to the fish, and swim speed were simultaneously monitored. No relationship was found between speed and muscle temperature, although metabolic heat production is inexorably linked to the former. Because both direct and inverse muscle temperature/heat production relationships were observed, and because physical (as opposed to physiological) explanations for our data can be discounted, we hypothesize yellowfin tuna are capable of some type of central nervous system (CNS)-mediated physiological thermoregulation.

INTRODUCTION

Although it is undisputed that tunas and lamnid sharks are warm bodied, no consensus has been reached on whether their muscle temperature can be regulated. Can these fish modify internal temperature without seeking more favorable external temperatures? Behavioral thermoregulation in the lower vertebrates is well documented, and indeed teleosts and reptiles possess a thermoregulatory center now considered homologous to that in the anterior forebrain of birds and mammals (Crawshaw 1977; Kluger 1978). Physiological ther-

moregulation is conceivable in tunas and lamnid sharks because they can maintain muscle temperatures significantly above T_a (Barrett and Hester 1964; Carey et al. 1971; Graham 1975; Stevens and Neill 1978).

Sustained elevated muscle temperatures are possible due to the presence of vascular heat exchangers and the internal position of the red-muscle-fiber portion of the myotomes (hereafter referred to as red muscle) (Carey et al. 1971; Erskine and Spotila 1977). Venous blood, warmed by metabolic heat, transfers this heat to the arterial blood in five plexi, formed from the dorsal aorta and posterior vena cava; from the epaxial, lateral cutaneous artery and vein; and from the hypaxial, lateral cutaneous artery and vein (Kishinouye 1923; Godsil and Byers 1944; Stevens, Lam, and Kendall 1974; Graham 1975); thus heat is retained within the red muscle.

Vascular heat exchangers are the anatomical characteristics which distinguish the tunas (Thunnini) from the other members of the family Scombridae, which include the mackerels (Scombrini),

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the Spanish mackerels (*Scomberomori*), and the bonitos (*Sardini*) (Collette 1978). All the true tunas maintain muscle temperature significantly above T_a .

Elevated muscle temperatures are thought to provide greater muscle power (Binkhorst, Hoofd, and Vissers 1977) and permit higher maximum swim speeds (Wardle 1975, 1977; Brill 1978). Also, heat exchangers give tunas a so-called thermal inertia far in excess of other teleosts of equal size (Neill and Stevens 1974; Neill, Chang, and Dizon 1976). Yet the advantages conferred by the specialized circulatory system and internal red muscle are still a matter of speculation (Stevens and Neill 1978).

There may be a disadvantage. At low activity, the excess temperature of the red muscle may be beneficial, but, because heat production is roughly proportional to the cube of swim velocity (Ware 1978; Wu and Yates 1978), at high activity muscle temperature could theoretically rise to deleterious levels (Sharp and Vlymen 1978). Thus, it is likely that tunas have the ability to control their thermoconserving mechanisms. Yet documentation of this ability is lacking.

Carey and Teal (1969) demonstrated that the difference between red-muscle temperature and water temperature (excess temperature or T_x) of recently captured bluefin tuna, *Thunnus thynnus*, was inversely proportional to sea-surface temperature. Red-muscle T_x of this fish varied only 5 C over a sea-surface temperature range of 10–30 C. Barrett and Hester (1964) showed the T_x of skipjack tuna, *Katsuwonus pelamis*, and yellowfin tuna, *T. albacares*, were maintained at approximately a fixed level above T_a . Carey et al. (1971) assumed the latter two species to be less adept at thermoregulation than bluefin tuna.

We feel data from recently captured fish are not compelling evidence for or against thermoregulatory ability for the following reasons. (1) The fish experienced an unknown thermal history prior to capture. Conceivably, tropical fish could have swum at greater depths, experiencing cooler temperatures than their more temperate conspecifics. Estimation of T_x based on sea-surface temperature would give a false impression of the ability to control muscle T_x . (2) The fish had an unknown activity history. Perhaps tropical tunas are less active prior to and during capture. Since metabolic heat production is almost a cubic function of velocity (Ware 1978; Wu and Yates 1978), activity level could be a prime determinant of muscle temperature. (3) Once boated, the reduced rate of heat transfer in air, effects of water evaporation, radiant heat exchange, and circulatory-pattern modifications may have an influence on muscle temperature.

Carey and Lawson (1973) presented what appeared to be direct evidence of a mammalian type of thermoregulation. They observed a free-swimming bluefin tuna that maintained a relatively constant stomach temperature during an 11 C change in water temperature. This fish, equipped with an ultrasonic telemetry device, dove from 19 C surface water into 5 C water, remained for 4 h, then returned to 13–14 C water. Stomach temperature did not change more than 2 C over the 4-h period spent in 5 C water. The authors concluded physiological thermoregulation. Subsequently, Neill and Stevens (1974) showed that no thermoregulatory ability need be postulated to explain the above data. Employing a constant coefficient of temperature change commensurate with the size of the animal and constant heat production, the temperature of the blue-

fin tuna was successfully modeled. Because no physiological processes influencing the rate of heat exchange needed to be included in the model, thermal inertia rather than thermoregulation was sufficient to explain Carey and Lawson's data.

Our current study is an extension of the efforts of Carey and his co-workers but is distinguished by a continuous record of swim speed and muscle temperature recorded under controlled environmental temperatures. In this report we demonstrate that swimming activity and red-muscle temperature are not inexorably coupled. This observation provides evidence that a mechanism exists for regulating metabolic heat dissipation. We elaborate these findings to suggest a conceptual model of physiological thermoregulation in tunas.

MATERIAL AND METHODS

Our experimental design employed equipment to determine swim speed and muscle temperature and to control seawater temperature. Fish were tested in a tank system consisting of an annular swim chamber equipped with photocells to determine fish position (and ultimately swim speed) and a heat exchanger that controlled water temperature, at either 20, 25, or 30 C. Red-muscle temperature of the fish was telemetered by a temperature-sensitive ultrasonic transmitter. Fish were tested individually using five consecutive 12-h temperature treatments (25, 20, 30, 20, and 25 C, or 25, 30, 20, 30, and 25 C), then killed, weighed, measured, and autopsied to verify thermistor position.

Yellowfin tuna (45.0–66.4 cm, fork length) were chosen from stocks maintained at 24 C in outdoor pools (7.3-m diameter $\times$ 1.2-m deep) at the Kewalo Research Facility of the Honolulu Laboratory of the National Marine Fisheries

Service. Nakamura (1972) has outlined details on capture, transportation, and maintenance of tuna stocks at this facility. We removed fish by angling with a barbless hook and transported them to the test tank in a plastic bag cushioned with a little seawater.

After transfer, the fish were rested for 2 h and then outfitted with the temperature-sensitive ultrasonic transmitter (generously supplied by Charles Coutant and James Rochelle, Oak Ridge National Laboratory). The transmitters (1.7-cm diameter $\times$ 3.4-cm length, 12 g in air) have a 10-cm long $\times$ 0.3-cm diameter probe containing the thermistor. The probe was inserted into the red muscle about 2 cm laterad to the origin of the first dorsal fin (fig. 1). The final thermistor position, later verified by dissection, was immediately adjacent to the vertebral column. Dart tags were inserted into the corselet and tied to the probe to secure the transmitter. After attachment of the transmitter, the fish was returned to the test tank; data collection began 2 h later.

The ultrasonic transmitter was designed for extended temperature monitoring from small fish (Rochelle and Coutant 1974). Temperature is telemetered by pulse-interval modulation, with the interval varying between 1,400 and 300 ms over a temperature range of 5–35 C. The transmitter was calibrated before deployment. Significantly, the calibration is not affected by a transmitter-thermistor temperature differential.

Transmitter output was received on a receiver-hydrophone system specially designed for underwater telemetry (CR-40, Communication Associates, Inc.).³ Pulse intervals were measured with a

³ Mention of trade names does not imply endorsement by the National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

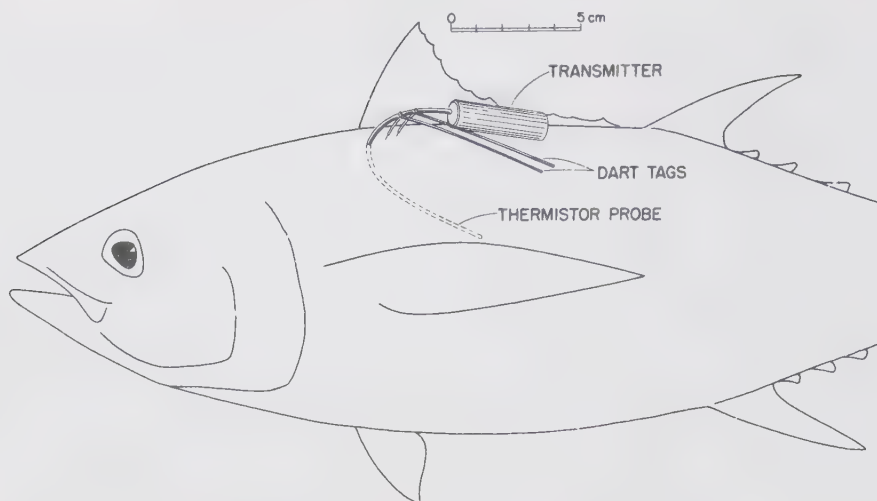


FIG. 1.—Tuna equipped with a temperature-sensitive ultrasonic transmitter for telemetering muscle temperature. The temperature-sensitive element lies immediately adjacent to the vertebral column.

frequency counter (HP 5300B/5308, Hewlett-Packard) and printed on paper tape (HP 5150) for later analysis. Precision of the telemetry system was approximately 0.05 C.

The fiberglass test tank (6.1-m diameter $\times$ 0.6-m deep) was fitted with a concentric inner wall so that the fish was constrained to swim in a 0.75-m wide $\times$ 0.61-m deep swim channel around the periphery. Six laps are equal to 100 m swum; swim speed was determined by lap times sensed with banks of photocells in each of the four tank quadrants. Water was introduced (and removed) from the swim chamber via two pairs of concentric polyvinyl chloride pipes positioned on the floor of the swim chamber. Entering (and exiting) water was divided into the paired pipes so that distribution of the temperature-controlled water to all parts of the tank was equal and no longitudinal temperature gradients developed. The seawater was recirculated at 1,136 liters/min through an outside stainless steel heat exchanger, and new seawater was added at about 38 liters/min. Temperature was generally regu-

lated within 0.05 C by 12 7.5-kW heaters and a 36.5-kW chiller. Maximum rate of seawater temperature change approached 0.1 C/min.

RESULTS

Six yellowfin tuna (fish 1–6) were individually subjected to consecutive 12-h temperature treatments: 25, 20, 30, 20, and 25 C. Fish 4 refused to swim laps after the first 30 C test period. Its data are incomplete since translation of position information into swim speed requires complete laps. Six other fish (7–12) experienced an altered temperature sequence (25, 30, 20, 30, and 25 C); four fish died (fish 9–12) during the second temperature period (30 C) and one (fish 8) during the third period (20 C). Data from fish 9–12 were discarded. The reason for mortality with the later test temperature sequence is not known.

Swim speed and water temperature were printed on paper tape every time the fish completed a lap (approximately every 20–30 s). For fish 1–6, red-muscle temperature was recorded every 10 min. Then, acquisition of a HP 9825A com-

puter allowed red-muscle temperature and water temperature to be recorded approximately every 30 s for fish 7 and 8.

Figure 2 presents a time series of the consecutive temperature treatments and swim speeds for fish 5, the largest fish tested. Note that, during water-temperature changes (approximately 0.1 C/min), red-muscle temperature changed also, but not as fast. This reflects the significant thermal inertia of tunas (Neill and Stevens 1974; Neill et al. 1976). Thermal inertia is also responsible for the periods during tank heating when body temperature was actually cooler than water temperature. The 30 C test period is most interesting. Here, the fish swam significantly faster than at 20 or 25 C, but red-muscle temperature decreased relative to water temperature. As noted, heat production is proportional to approximately the cube of swim speed (Ware 1978; Wu and Yates 1978). Therefore, if the fish could not adjust their thermoconserving mechanisms, muscle temperature should have increased.

We calculated the mean and standard deviation for swim speed (and red-muscle temperature for fish 7 and 8) for each 10-min period. Table 1 lists the

grand means for each temperature treatment (and 95% confidence limits) based on the 10-min means (single 10-min red-muscle-temperature readings for fish 1–6). Means are based only on data recorded during the final 8 h of the 12-h temperature treatment, in order to minimize the effects of previous temperature levels. Four hours is sufficient time for tunas of these sizes to reach thermal equilibrium (Neill et al. 1976).

Table 1 presents the summarized data on individual fish. In most cases, the pattern is similar to that of fish 5. During the 30 C test period, the tunas swam faster but had lower excess red-muscle temperatures. Fish 6 is an exception. Perhaps this fish was not thermoregulating, because muscle temperature and swim speed appear correlated.

The data from fish 7 (tested under the 25, 30, 20, 30, and 25 C temperature sequence) were also significantly different from those for the other fish. During the first 30 C test period mean swim speed was 62.70 cm/s, and mean excess red-muscle temperature was 0.54 C. During the single 20 C test period mean swim speed decreased to 43.16 cm/s, but mean red-muscle excess temperature remained at 0.51 C. During the second

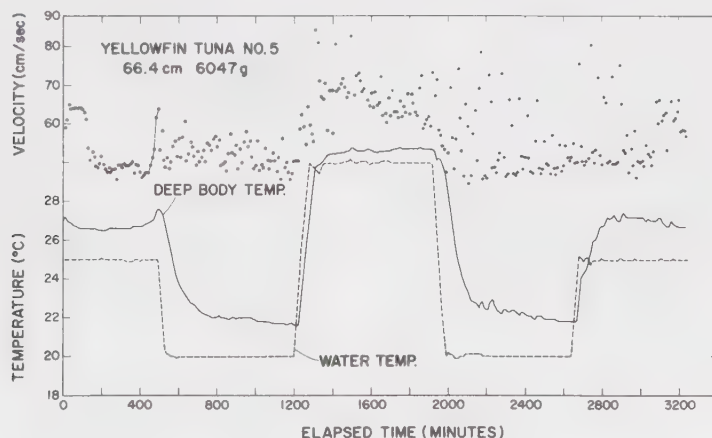


FIG. 2.—Time series of muscle temperature, water temperature, and swim speed of a yellowfin tuna

TABLE 1
SUMMARY OF EXPERIMENTAL RESULTS

Fish	FORK LENGTH (cm)	WEIGHT (g)	TEST TEMPERATURES (°C)				
			25	20	30	20	25
Fish 1.....	45.9	1,853					
Swim speed (cm s ⁻¹).....			55.00 ± 1.06	45.55 ± .36	65.61 ± 1.30	43.68 ± 1.16	50.47 ± 1.34
Temperature excess (°C).....			1.34 ± .03	1.07 ± .02	.94 ± .01	1.55 ± .05	1.24 ± .06
Estimated heat production (W).....			2.72	2.53	2.98	2.50	2.61
Fish 2.....	47.8	2,219					
Swim speed (cm s ⁻¹).....			67.88 ± 1.56	67.34 ± 1.27	84.82 ± 2.56	61.32 ± 1.77	73.70 ± 1.37
Temperature excess (°C).....			1.47 ± .02	1.28 ± .03	.62 ± .01	1.15 ± .04	1.48 ± .03
Estimated heat production (W).....			3.40	3.43	4.04	3.22	3.63
Fish 3.....	45.5	2,677					
Swim speed (cm s ⁻¹).....			51.70 ± 1.32	51.13 ± .28	77.48 ± 1.65	54.17 ± .21	55.10 ± 1.48
Temperature excess (°C).....			1.30 ± .09	1.38 ± .01	1.05 ± .04	1.24 ± .04	1.42 ± .04
Estimated heat production (W).....			3.13	3.15	3.88	3.22	3.21
Fish 4.....	48.3	1,942					
Swim speed (cm s ⁻¹).....			55.67 ± .89	46.54 ± 1.28	57.91 ± 2.72		
Temperature excess (°C).....			1.75 ± .05	1.43 ± .04	.90 ± .02		
Estimated heat production (W).....			2.84	2.64	2.86		
Fish 5.....	66.4	6,047					
Swim speed (cm s ⁻¹).....			52.38 ± 1.54	51.17 ± .96	66.89 ± 1.55	52.28 ± 2.24	57.79 ± 2.41
Temperature excess (°C).....			1.72 ± .06	1.87 ± .05	.63 ± .02	2.16 ± .09	1.85 ± .10
Estimated heat production (W).....			5.07	5.07	5.70	5.11	5.30
Fish 6.....	45.0	1,491					
Swim speed (cm s ⁻¹).....			67.52 ± .61	47.88 ± 1.81	61.52 ± 1.07	44.11 ± .76	49.72 ± 1.02
Temperature excess (°C).....			.99 ± .13	.27 ± .06	.64 ± .02	.43 ± .01	.76 ± .01
Estimated heat production (W).....			2.82	2.32	2.59	2.24	2.34
Fish 7.....	53.0	2,237					
Swim speed (cm s ⁻¹).....			67.08 ± 1.27	62.70 ± .77	43.16 ± .34	56.37 ± .53	58.35 ± 1.38
Temperature excess (°C).....			.64 ± .09	.54 ± .02	.51 ± .03	.74 ± .04	.76 ± .02
Estimated heat production (W).....			3.91	3.66	3.14	3.44	3.56
Fish 8.....	65.0	3,797					
Swim speed (cm s ⁻¹).....			42.83 ± .55	83.39 ± 4.13			
Temperature excess (°C).....			.81 ± .02	.66 ± .04			
Estimated heat production (W).....			3.74	5.74			

NOTE.—95% confidence limits are provided for mean swim speeds and temperature excess. To insure the fish were in thermal steady state, mean excess temperatures are based on readings from the last 8 h of each test period. Heat production is estimated using biological parameters of swim speed, weight, length, and muscle efficiency as well as temperature-dependent properties of viscosity and density of the seawater.

30 C period, mean swim speed increased to 56.37 cm/s, and mean excess red-muscle temperature increased to 0.74 C.

From the data, it is clear that red-muscle temperature is not inexorably linked to swim speed (as suggested by Sharp and Vlymen 1978). Previous work with skipjack tuna under identical conditions demonstrated a similar independence, rather than a direct or inverse relationship, of muscle temperature and swim speed (Dizon, Brill, and Yuen 1978).

WHOLE-BODY THERMAL CONDUCTANCE

To quantify thermoregulatory ability, mammalian physiologists (e.g., Kleiber 1972) often employ an index of whole-body thermal conductance. The concept is based on the equation:

$$H_L = K \cdot (T_c - T_a) \quad (1)$$

where H_L = steady-state heat loss (i.e., T_c is not changing, therefore H_L must equal heat production) (W), T_c = the temperature of the isothermal core (C), T_a = ambient temperature (C), and K = whole-body thermal conductance (W/C). The K is a lumped parameter which reflects properties of both the animal and the environment (Strunk 1971, 1973; Tracy 1972). In an aquatic environment, heat transfer due to radiation and evaporation can be ignored (Erksine and Spotila 1977). Thermal conditions are, therefore, adequately defined by water temperature and the velocity of the animal relative to the water. In addition, since comparisons are made between temperature treatments, not fish, we are not concerned with the absolute value of K but, rather, with how this parameter varies with changes in T_a .

We measured steady-state red-muscle and water temperatures. Therefore, by estimating heat production, we can use

the concept of K (eq. [1]) to quantify the thermoregulatory ability of our yellowfin tuna. To estimate the heat production of the fish, we proceeded as follows: metabolic energy required for propulsion is related to swim velocity by the following fundamental equation (see Webb 1975; Sharp and Francis 1976; Ware 1978; Wu and Yates 1978 for a more detailed development):

$$\eta \cdot P_1 = 0.5 \rho \cdot V^3 \cdot S \cdot C_d \cdot 10^{-7}, \quad (2)$$

where P_1 = rate of free energy liberation by the swimming muscles (W); ρ = density of seawater (g/cm³); V = mean swim velocity (cm/s); S = surface area ($\sim 0.4 L^2$) (cm²); L = fork length (cm); C_d = coefficient of drag, a dimensionless number (this parameter takes into account the effect of temperature on seawater viscosity); and η = muscle efficiency, assumed equal to 0.20 (Webb 1975).

Brill (1979) determined the standard metabolic rate (i.e., metabolic rate associated with nonswimming physiological functions, such as osmoregulation and cardiac work) by measuring the oxygen consumption of skipjack tuna (at 24–26 C) with no overt muscular activity. The relationship, converted to power units, is:

$$P_2 = 1.53 W^{0.563}, \quad (3)$$

where P_2 = standard metabolic rate (W) and W = fish weight (kg).

Because no data for the yellowfin tuna standard metabolic rate are yet available, we assume this relationship to be a suitable approximation. Furthermore, we rejected use of a temperature correction to P_2 ; i.e., we assumed P_2 , the standard metabolic rate, to have a $Q_{10} = 1$. We realize that this is unlikely, but we have no data on the effect of temperature on tuna standard metabolic rate. Assuming that the $Q_{10} > 1$ results

in proportionally greater heat production at higher test temperatures and, consequently, higher estimated K . Use of a P_2 which is independent of temperature is conservative with respect to our hypothesis.

Heat production within the fish (H_p) can be estimated by adding the standard metabolic rate to the muscular heat production due to swimming. The latter quantity is determined by assuming the caudal propeller is 100% efficient and the swimming muscles 20% efficient (i.e., $\eta = 0.20$). The H_p is therefore approximated by the sum of the two power-producing processes, less the power dissipated as thrust:

$$H_p = P_2 + (1 - \eta)P_1. \quad (4)$$

We substituted estimated H_p (based on V), mean red-muscle temperature, and water temperature into equation (1). Results are presented in figure 3. In fish 1-5 and 8, increased thermal conductance was observed at the 30 C test temperature. This temperature is close to the upper limit of occurrence of the species (31 C [Blackburn 1965]). Also, for fish 1-5, K was reasonably constant at 20 and 25 C. Fish 6 and 7 showed no apparent pattern. These results indicate

that faster swimming (which must increase H_p) does not necessarily increase red-muscle temperature because some mechanism intervenes to alter the pattern of thermal transfer, which is reflected by changes in K .

DISCUSSION

We have no reliable method for experimental control of swim speed. Because the fish were swimming near their minimum hydrostatic equilibrium speeds (Magnuson 1973), excess red-muscle temperatures are low when compared with wild fish (Barrett and Hester 1964; Stevens and Fry 1971; Graham 1975). However, the differences in swim speeds and excess muscle temperatures between temperature treatments are statistically significant. Presumably, if our yellowfin tuna were forced to swim at elevated speeds, the reductions of the resultant higher excess muscle temperature would have been more dramatic as test temperatures rose. We have already shown this to occur in skipjack tuna, *Katsuwonus pelamis*, forced to maintain elevated swim speeds at 25 and 30 C (Dizon and Brill 1979).

At least four mechanisms could account for the apparent increase in K

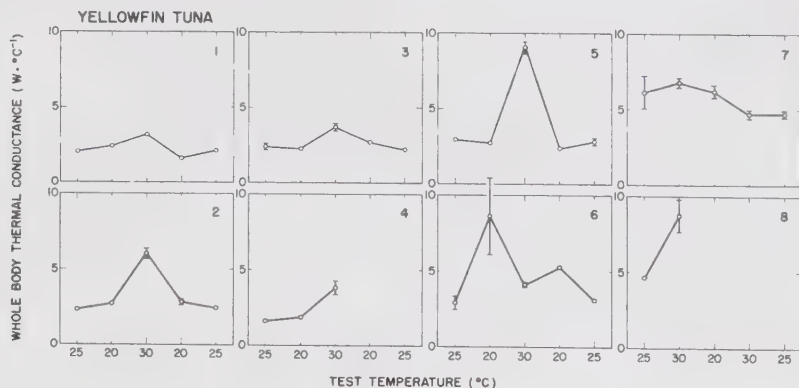


FIG. 3.—The effect of T_a on whole-body thermal conductance (K). The K was determined by dividing estimated heat production by excess muscle temperature (T_x). Vertical lines represent extreme values of K based upon the 95% confidence limits of mean swim speed and T_x .

that would not constitute physiological thermoregulation per se. Each is considered below and can be discounted.

1. Propulsive musculature of yellowfin tuna may be more thermally efficient (i.e., produce less heat per unit energy provided to the caudal propeller) at higher T_a 's. If so, we would be overestimating H_p at 30 C and inflating the value of K . Using fish 5 as an example, the following calculations show η would have to be unreasonably increased for the values of K determined at 25 and 30 C to be equal. Here we will even ignore the heat production from nonswimming physiological functions (SMR):

$$K = H_p \cdot T_x^{-1}, \quad (5)$$

$$H_p = (1 - \eta) \cdot P_1, \quad (6)$$

$$\therefore K = (1 - \eta) \cdot P_1 \cdot T_x^{-1}, \quad (7)$$

and

$$P_1 = (0.5 \cdot \rho \cdot V^3 \cdot S \cdot C_d \cdot 10^{-7}) \cdot \eta^{-1}. \quad (8)$$

Substituting equation (8) into (7) yields:

$$K = (1 - \eta) \cdot (0.5 \cdot \rho \cdot V^3 \cdot S \cdot C_d \cdot 10^{-7}) \cdot (\eta \cdot T_x)^{-1}. \quad (9)$$

Substituting the average velocity (66.89 cm s⁻¹) and excess muscle temperature (0.63 C) for yellowfin 5 at 30 C and the K value at 25 C (0.458 W C⁻¹, when the SMR is not included) into equation (9) shows η would have had to increase from 20% at 25 C to 55% at 30 C. This is unlikely, especially since the SMR contribution to H_p is considerable.

2. Any effects of seawater viscosity or density changes are taken into account in equation (2). The H_p would not be over- or underestimated due to temperature-induced changes in these parameters.

3. If the main resistance to heat flow occurred at the body surface-water interface, increased swim speed could

result in lower excess red-muscle temperature because a higher rate of water flow over the body surface would cause increased surface heat loss (Tracy 1972; Erskine and Spotila 1977; Brill, Guernsey, and Stevens 1978). In other words, increased swim speed would cause increased convective-enhanced surface conductance (Strunk 1973), and, at higher swim speeds, the requisite increase in heat loss could then be accomplished with a lower temperature driving gradient (i.e., lower excess red-muscle temperature).

However, as we have stated, H_p is roughly proportional to velocity cubed, whereas surface heat loss at best increases only as the square root of velocity (Erskine and Spotila 1977; Sharp and Vlymen 1978). Therefore, increased convective-enhanced surface conductance could not account for our data. If water velocity was the main determinant of K , a direct and nonlinear relationship between swim speed and excess muscle temperature would be predicted. We, however, observed a direct relationship in only one of eight fish.

Furthermore, a mathematical model developed by Sharp and Vlymen (1978) describing the relationship of excess muscle temperature and swim speed in yellowfin and skipjack tunas predicts that these fish will develop lethal muscle temperature at upper sustainable swim speeds unless the effectiveness of their thermoconserving mechanisms can be reduced.

4. Because increased swim speed requires increased cardiac output and the effectiveness of a countercurrent heat exchanger is inversely proportional to flow (Mitchell and Myers 1968), tuna then should show an inverse relationship between excess muscle temperatures and swim speeds. This concept does seem to fit some of our data (e.g., fish 4, 5, and

8) and, since no central nervous system (CNS)-mediated conductance changes are required, we may have no proof of activity-independent thermoregulation. However, the data presented here (see also Dizon et al. 1978; Dizon and Brill 1979) clearly show swim speed and excess red-muscle temperature have no fixed relationship, either direct or inverse.

POSSIBLE MECHANISMS OF PHYSIOLOGICAL
THERMOREGULATION

The lack of any predictable relationship between red-muscle temperature and swim speed strongly suggests that we are dealing with physiologically labile processes, presumably under CNS control. Tunas face two situations where changes in the patterns of heat transfer are required: (1) excess red-muscle temperatures must be reduced in response to increases in seawater temperatures; and (2) increased H_p , due to increased swim speed, must be effectively dissipated to prevent development of potentially lethal T_b 's. We hypothesize that these two exigencies could be met either with changes in circulatory patterns, alterations in the relative contributions of the red- and white-muscle fibers to propulsion, or both.

The second exigency, prevention of overheating during bouts of fast swimming, presents no conceptual problem if one discards the notion that the white muscle is only used at high unsustainable speeds (only used anaerobically). White muscle of skipjack tuna has the enzymatic capacity to function aerobically (Hochachka, French, and Guppy 1978) and apparently becomes active at sustainable swimming velocities (3–5 lengths/s, based on electromyographic evidence [Brill and Dizon, in preparation]). Other teleosts have also been shown to use white muscle at sustainable

swim speeds (Pritchard, Hunter, and Lasker 1971; Bone 1975). White muscle of *Thunnus* sp. is supplied by circulatory pathways which bypass the heat exchangers (Godsil and Byers 1944); therefore, metabolic heat generated aerobically by the white muscle is not retained but dissipated in the same manner as in nonthermoconserving fish, via the gills and the body surface (Stevens and Sutterlin 1976; Erskine and Spotila 1977).

Unless heat-exchanger efficiency could be reduced, the contribution of red muscle to propulsion would probably be limited to power-production levels which will not generate damaging temperatures. Small tunas do not appear to overheat; in tests of chased fish either carrying telemetry equipment or dragging thermistor wires, muscle temperatures were never observed above 32°C (Neill et al. 1976; Hulbert and Guppy, personal communication, 1978).

Control of excess muscle temperature extends beyond prevention of overheating; observations have been made here and in other reports (Barrett and Hester 1964; Carey and Teal 1969) that tunas reduce their muscle temperatures in response to increasing water temperatures (the first exigency). We imagine two mechanisms that the fish might employ. (1) Modification of the circulatory pattern in the central or lateral heat exchangers may reduce their effectiveness as thermal barriers. Changes in water temperature and activity levels have been shown to affect teleost cardiovascular dynamics by simultaneously increasing the level of vagal activity and circulating catecholamines (Randall 1970; Stevens et al. 1972; Watters and Smith 1973). Furthermore, Stevens et al. (1974) show the arterial vessels of the central heat exchanger in skipjack tuna have thick walls containing smooth muscle. If moderate in-

creases in T_a or swim speed cause a sympathetically controlled release of catecholamines, change in vagal activity, or both, a modification of the circulatory pattern within the central or lateral heat exchangers could result, diminishing their effectiveness. (2) The relative contribution of red and white muscle to propulsion at slow speeds might be under the control of the thermoregulatory center. At high T_a 's white muscle, which does not contribute to the temperature burden, may become active at slower swim speeds than it would at low T_a 's.

The former thermoregulatory mechanism would presumably be more important in skipjack tuna and kawakawa, *Euthynnus affinis*, because, in these species, the lateral cutaneous blood vessels are much smaller than the dorsal aorta and postcardinal vein. Unless the lateral cutaneous vessels are extremely distensible, it is unlikely that they could carry enough blood to the segmental vessels to maintain a significant level of aerobic metabolism in the white muscle.

SUMMARY

Tunas have developed a degree of independence between red-muscle temperature and swim speed even though H_p is inexorably linked to the latter. We have observed this independence in yellowfin tuna (this report) and skipjack tuna (Dizon et al. 1978). Furthermore, six of the eight yellowfin tuna used in this study showed significantly lower excess muscle temperatures at 30 C than at 20 or 25 C, although their mean swim speeds were significantly increased at the higher T_a .

Data exist demonstrating that white muscle has significant aerobic enzymatic capacity (Hochachka et al. 1978), is used at apparently sustainable swim speeds (Brill and Dizon, in preparation), and has a circulatory system which bypasses the vascular countercurrent heat exchangers (at least in *Thunnus* sp. [Godsil and Byers 1944]). Excess muscle temperatures observed in tuna must be wholly due to heat produced and retained in the red muscle. Here, heat dissipation is limited by its internal position, surrounded by white-muscle fibers and by the five vascular heat exchangers interposed in the circulatory system serving the red-muscle fibers. Based on a mathematical model of H_p and surface heat dissipation in skipjack and yellowfin tunas (Sharp and Vlymen 1978), we hypothesize that, at sustained elevated swim speeds (3–6 body length s^{-1}), red-muscle fibers must contribute a relatively small fraction of the necessary power; otherwise, overheating could result.

Tunas therefore face two exigencies that require adjustment of their thermoregulating mechanisms. One, excess muscle temperature must be reduced at T_a 's near lethal limits. Two, the fraction of metabolic H_p lost via the gills must be significantly increased at the higher sustainable swim speeds. We suggest that tuna meet these two thermoregulatory exigencies either by: (1) using their white-muscle fibers at upper sustainable swim speeds and at low swim speeds when T_a 's approach lethal limits; or (2) using cardiovascular alterations that diminish or enhance their vascular heat exchanger's effectiveness; or both.

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CONVERSION ALGORITHMS FOR THE CALCOFI STATION GRID

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ABSTRACT

This note presents algorithms which may be used to convert station positions expressed in geographic coordinates (latitude and longitude) to the California Cooperative Oceanic Fisheries Investigations (CalCOFI) station grid coordinates and vice versa. Clarke's spheroid of 1866 is used as an estimate of the geoid off the west coast of North America.

INTRODUCTION

The CalCOFI station pattern (Figure 1) was designed originally in the development of a systematic sampling program to determine the major spawning areas of the Pacific sardine off the coasts of the United States and Baja California, Mexico. Surveys were conducted along lines extending seaward approximately normal to the coast and spaced 120 miles apart from the Columbia River to Sebastian Vizcaino Bay. As the program progressed and spawning areas were delimited, additional lines of stations were added between the cardinal lines, and the surveys became concentrated off the coasts of California and Baja California.

The pattern was based on line 80 off Point Conception, California. Other lines were numbered using increments of 10, decreasing northwestward to line 10 off the U.S.-Canadian border, and increasing southeastward to line 157 off Cape San Lucas, Baja California (Kramer et al. 1972). It was originally intended that the 120-mile spacing would allow for additional lines to be plotted 12 miles apart between the cardinal lines and still be designated by whole numbers without resorting to fractions. However, when it was decided to insert additional lines, 40-mile intervals appeared to be sufficient. Thus the major pattern consists of cardinal lines in numbered multiples of 10 and ordinal lines whose numbers by convention end in 3's and 7's, having been rounded off from 3.333. . . . and 6.666. . . .

The stations on the lines were laid out on the basis of a perpendicular to line 80, through a point designated Station 80.60. The original stations were plotted 40 miles apart and were numbered by increments of 10, which allowed additional stations between the 40-mile points to be plotted as close to 4 miles and still be designated by whole numbers.

CONVERSION OF CALCOFI GRID COORDINATES TO GEOGRAPHICAL COORDINATES

The primary reference point, Station 80.60, was located at 34°09'N, 121°09'W and is marked 0 in Figure 1. The perpendicular to line 80, through this point, was used to set all the other lines and will be referred to in the following discussion as the reference line.

As indicated before, unit line number increments represent 12 nautical miles and unit station number increments represent 4 nautical miles. Therefore, to locate a particular station, such as 50.120 (designated P in Figure 1), one would first proceed 360 nautical miles northwestward along the reference line from the reference point to Station 60 on line 50 (designated R in Figure 1), and then 240 nautical miles southwestward on line 50 to Station 120.

The CalCOFI station plan was originally laid out in this manner with the aid of navigation and plotting charts. CalCOFI station locations can also be computed numerically, using the Mercator transform based on Clarke's spheroid of 1866, as given by Bowditch (1958). The numerical procedure can be derived from the geometry of Figure 1, bearing in mind that distance along the Y-axis (north-south) on a Mercator chart must be measured in meridional units rather than in units of latitude.

Let PLA	=	Latitude of P
PLO	=	Longitude of P
PLN	=	Line number of P
PSN	=	Station number of P
RLA	=	Latitude of R
MCTR(LA)	=	Mercator transform

which expresses the distance from the equator to latitude LA and is defined by:

$$MCTR(LA) = (180/\pi) * (\ln(\tan(45 + LA/2)) - 0.00678766 * \sin(LA))$$

This is an approximation, accurate to within 3 seconds (in meridional units) south of 60° N. Recalling that the CalCOFI coordinates of the primary reference point are 80 (line number) and 60 (station number) and the geographical location of this point is 34°09'N, 121°09'W, the following sequence can be used to compute the location of P.

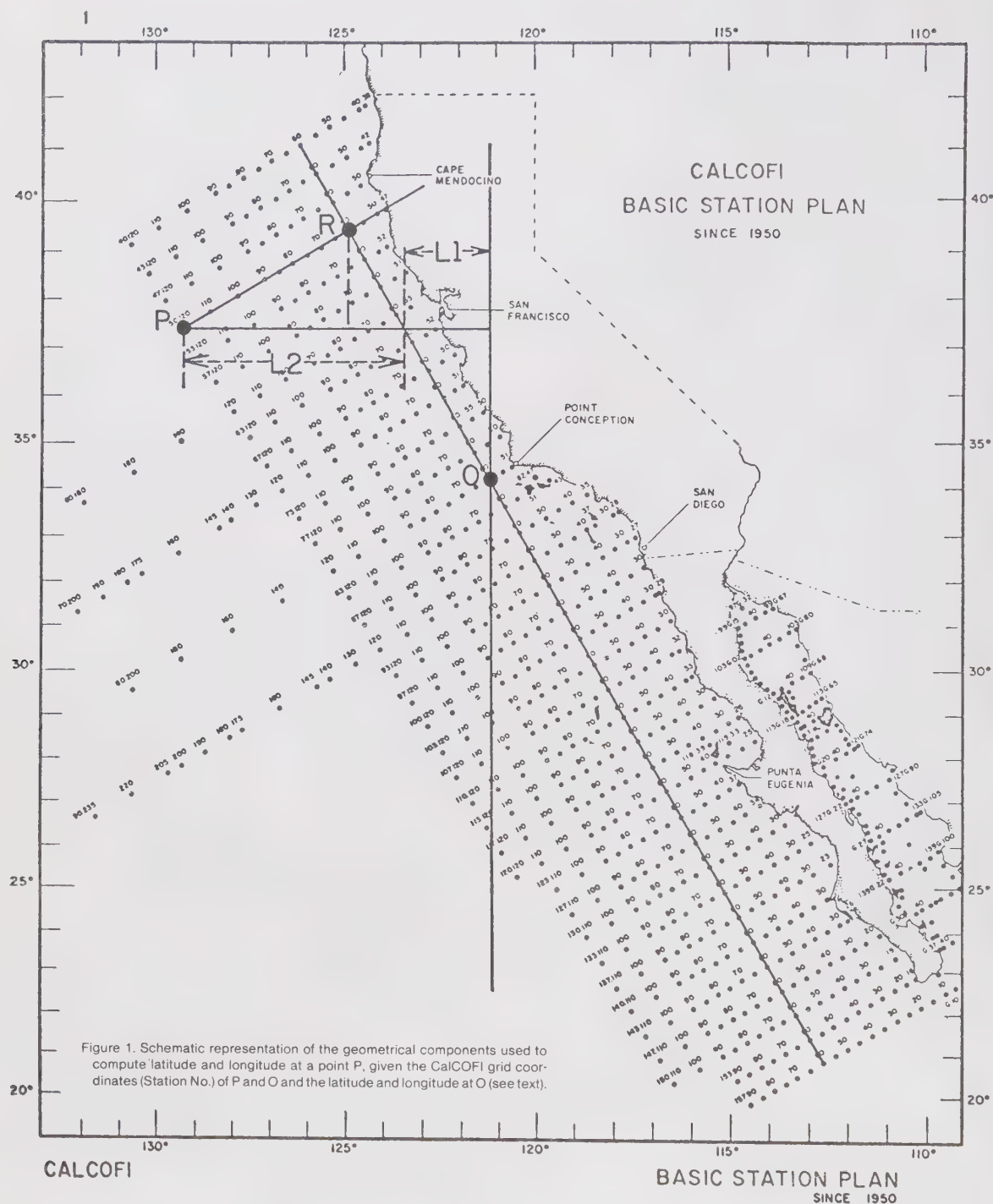


Figure 1. Schematic representation of the geometrical components used to compute latitude and longitude at a point P, given the CalCOFI grid coordinates (Station No.) of P and O and the latitude and longitude at O (see text).

1. $RLA = 34.25 - 0.2 \cdot (PLN - 80) \cdot \cos(30)$
2. $PLA = RLA - (1/15) \cdot (PSN - 60) \cdot \sin(30)$
3. $L1 = (MCTR(RLA) - MCTR(34.15)) \cdot \tan(30)$
4. $L2 = (MCTR(RLA) - MCTR(PLA)) / (\cos(30) \sin(30))$
5. $PLO = L1 + L2 + 121.15$

CONVERSION OF GEOGRAPHICAL COORDINATES TO CALCOFI COORDINATES

The computation of CalCOFI line and station numbers for a given location where latitude and longitude are given requires determination of a latitude when its Mercator transform is known, i.e. given $MCTR(LA)$, find (LA) . There is no simple algebraic solution to this problem; however, (LA) can be approximated with as much precision as desired with a simple iterative procedure in which $MCTR(LA)$ is entered as the first approximation to (LA) . The algorithm for the inverse Mercator transform is as follows:

1. Set $I = 0$
2. Set $LA = MCTR(LA)$
3. $LA = 2 \cdot (\arctan(\exp(MCTR(LA) \cdot \pi / 180 + 0.00676866 \cdot \sin(LA))) - 45)$
4. $I = I + 1$
5. IF $I < 3$ GO BACK TO STEP 3
6. STOP

The CalCOFI grid coordinates for a station at a given location can be computed with the following sequence:

1. $L1 = (MCTR(PLA) - MCTR(34.15)) \cdot \tan(30)$
2. $L2 = PLO - L1 - 121.5$
3. $MCTR(RLA) = L2 \cdot \cos(30) \sin(30) + MCTR(PLA)$
4. $RLA = \text{INVERSE}(MCTR(RLA))$
5. $PLN = 80 - (RLA - 34.15) \cdot 5 / \cos(30)$
6. $PSN = 60 + (RLA - PLA) \cdot 15 / \sin(30)$

DISCUSSION

The two conversion procedures presented here are mutually consistent in that when executed consecutively, using the output from one run as input for the next, the original coordinate values can be recovered with a precision of at least four decimal places. For example, Station 50.120 converts to $37^\circ 20.7692'N$, $129^\circ 16.7727'W$. With these values as input, the reciprocal conversion yields 50.0000 and 120.0000 for line and station, respectively. However, if the geographical coordinates are rounded to tenths of minutes, as is common in CalCOFI work, the conversion to line and station becomes 49.9969 and 120.0004.

We should point out that the correspondence between CalCOFI and geographical coordinates as computed from the numerical procedures is not in exact agreement with that given in the standard reference tables used by CalCOFI. The discrepancies are generally less than 2 minutes of latitude or longitude for given CalCOFI station numbers except out on the fringes of the pattern. They may possibly be due to accumulative errors incurred when laying out the station pattern on the navigational charts.

It should further be noted that even greater discrepancies are found when the computed locations for CalCOFI stations are compared with the actual locations occupied on individual cruises, as reported in the CalCOFI Physical and Chemical Data Reports. Deviation from standard station positions may have occurred during CalCOFI cruises to avoid navigational hazards or other reasons and nearby alternate locations accepted as representing the designated station. The conversion procedures can provide a convenient way to determine the CalCOFI coordinates of the actual locations occupied in such instances.

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ASSOCIATIONS OF TUNA WITH FLOTSAM IN THE EASTERN TROPICAL PACIFIC

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ABSTRACT

The fishing record for flotsam-associated tuna in the eastern tropical Pacific was examined. The rivers of Central America are probably the major source of flotsam. Correlation analysis of the number of sets occurring in an area indicates that unassociated tuna and flotsam-associated tuna are related. The number of sets made on floating objects has increased dramatically since 1971. The percentage of flotsam-associated sets has increased, indicating that flotsam-associated sets are more important to the tuna fishery than in 1963. The catch per set of tuna associated with flotsam has also increased markedly since 1967. Analysis of length-frequency data indicate that, on a single set basis, tuna fork length is more variable in sets associated with flotsam than with unassociated schoolfish sets. Results of the length-frequency analysis support the idea that flotsam aggregates tuna.

The catch of the eastern tropical Pacific tuna fishery consists of mostly yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*. The catch is frequently categorized by the conditions under which the purse seine set is made. Scott (1969) made a major distinction between associated schools and unassociated schools. Associated schools are caught either in "porpoise sets" (sets associated with porpoise) or "floating object sets" (sets associated with logs or other flotsam). Unassociated schools are caught in "night sets" (sets made at night with the aid of bioluminescence) and "schoolfish sets" (schools seen and set upon during the day). Night sets compose a very small proportion of total sets and will not be discussed in this paper. Porpoise sets catch mostly yellowfin tuna. Floating object sets and schoolfish sets catch yellowfin and skipjack tuna, either as pure or mixed species.

Little is known about the attraction of tuna to flotsam. Gooding and Magnuson (1967) and Hunter and Mitchell (1968) observed fish gathering around flotsam. These authors attracted some tuna to their flotsam, but never large schools. Tuna were a minor portion of the observed fish assemblages. Hunter and Mitchell (1968) postulated a connection between schooling behavior and the attraction of fish to flotsam. They concluded that flotsam had the function of providing (p. 27) "... a visual stimulus in an optical void." Gooding

and Magnuson (1967) concluded that fish gathered around floating objects at sea primarily because the objects provided shelter from predation. It may be possible that the same factors attracting smaller fish also attract large tuna schools.

This paper examines historical tuna fishery data on the catches of yellowfin and skipjack tuna associated with floating objects in the eastern tropical Pacific from 1963 to 1975. The objectives of the paper are to 1) establish the main sources of flotsam, 2) determine if there is a connection between various set types, 3) see if flotsam-associated sets have become more important to the tuna fishery, 4) determine if the catch rate on flotsam-associated sets has changed, and 5) assess whether flotsam does aggregate tuna schools.

METHODS

Since the catch of tuna associated with flotsam depends on the presence of tuna, flotsam, fishermen, strength of attraction, and suitable fishing conditions, I examined each factor in light of the published literature and available fishery data from the eastern tropical Pacific tuna fishery.

The Inter-American Tropical Tuna Commission (IATTC) collects information from tuna fishermen operating in the eastern tropical Pacific. Information collected in logbooks includes date and location of sets, catch of various species, type of set, and environmental conditions. Although these logbooks remain confidential, it is possible to obtain summaries of the information for certain time-area strata. During the beginning portion of

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the year, yellowfin tuna fishing is unregulated. After a quota is reached (Table 1), all yellowfin tuna fishing, except for special allowances must be outside the Commission's Yellowfin Regulatory Area (CYRA) (Figure 1). Due to special rules (see

TABLE 1.—Yellowfin quota (thousands of short and metric tons), closure data, and annual total catch (thousands of short and metric tons) for the Commission's Yellowfin Regulatory Area, taken from Calkins (1976).¹ Metric tons are given in parentheses.

Year	Quota	Quota + increment ²	Closure date	Annual total catch
1966	79.3 (71.9)		Sept 15	91.1 (82.6)
1967	84.5 (76.6)		June 24	89.6 (81.3)
1968	106.0 (96.1)		June 18	114.6 (103.9)
1969	120.0 (108.8)		Apr. 16	126.5 (114.7)
1970	120.0 (108.8)		Mar. 23	142.6 (129.3)
1971	140.0 (127.0)		Apr. 9	113.9 (103.3)
1972	120.0 (108.8)	140.0 (127.0)	Mar. 5	152.5 (138.3)
1973	130.0 (117.9)	160.0 (145.1)	Mar. 8	177.8 (161.3)
1974	175.0 (158.7)	195.0 (176.9)	Mar. 18	191.3 (173.5)
1975	175.0 (158.7)	195.0 (176.9)	Mar. 13	177.2 (160.7)
1976	175.0 (158.7)	195.0 (176.9)	Mar. 27	205.5 (186.4)

¹Calkins, T. P. 1976. The 1976 fishing year (through August 30). Background Paper No. 1, 33rd meeting of the Inter-American Tropical Tuna Commission.

²The Director of IATTC may increment the established quota, allowing more yellowfin tuna to be caught.

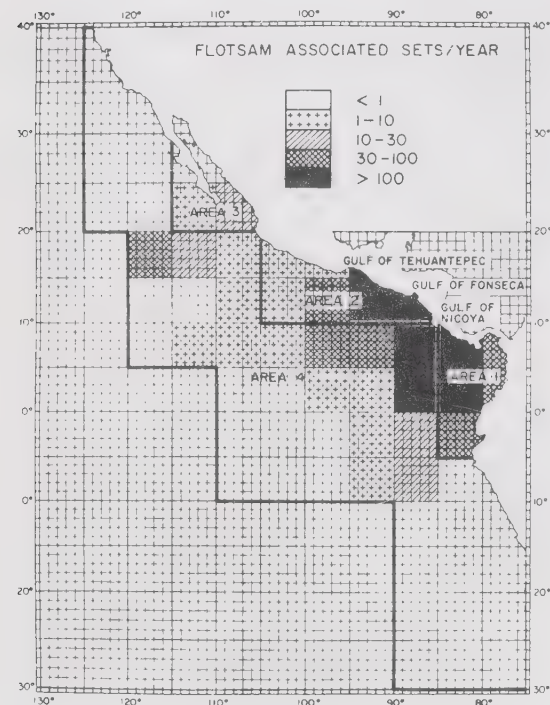


FIGURE 1.—Eastern tropical Pacific fishing area divided into three nearshore areas (Areas 1-3) and one offshore area (Area 4). The heavy line to the west delimits the boundary for the Commission Yellowfin Area (CYRA). The average number of flotsam-associated sets from 1972 to 1975 by 5° squares is shown. Data represent the unregulated fishing period (see text).

Inter-American Tropical Tuna Commission 1967-1975), any detailed reporting of regulated data would compromise the confidentiality of the data; hence, only unregulated catch and number of sets within the CYRA summarized by month and 5° square for 1963-75 were made available to me.

The total number of unregulated sets during the 13 yr was approximately 161,000 of which 8,190 were associated with flotsam. In addition, the IATTC provided the total number of flotsam-associated sets occurring each year (Figure 2). One sees that the major trends in the number of sets are contained in the block of unregulated data.

NOAA's Southwest Fisheries Center (SWFC) periodically sends technicians aboard tuna seiners. These technicians record details about set type, catch, environmental conditions, as well as the fork length (centimeters) of tuna sampled from individual sets. Fork lengths of yellowfin and skipjack tuna were only available for a limited number of sets made in 1973-75. The location of fork length measurements are given in Table 2. Single set catch data were collected by SWFC technicians in 1974-76 (unpubl. data²).

²Unpubl. data on file at the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

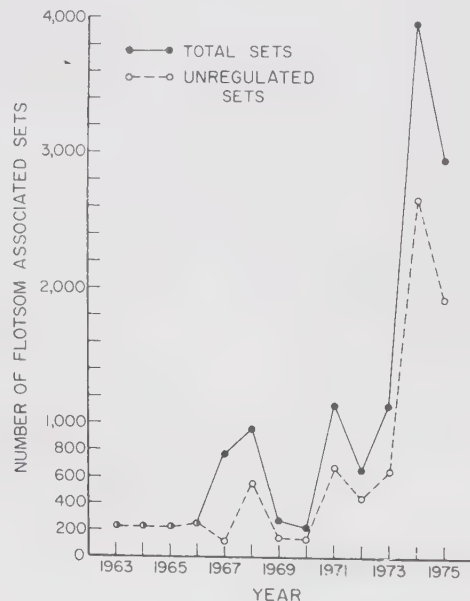


FIGURE 2.—Total number of flotsam-associated sets made in the eastern Pacific and number of unregulated flotsam-associated sets made in the CYRA, 1963-75.

TABLE 2.—Spatial distribution of fork length measurement (centimeters) of yellowfin and skipjack tuna in the Commission's Yellowfin Regulatory Area, 1973-75. CYRA subareas are shown in Figure 1. (Source of data, SWFC.)

CYRA subarea	Number of sets where fork length was measured
1	56
2	12
3	14
4	29

Monthly rainfall in Central America was calculated by averaging the stations reporting to the Environmental Data Service (U.S. Department of Commerce 1963-1975).

In order to achieve the objectives of this paper, the data obtained from IATTC and SWFC were examined and analyzed in several ways. The main sources of flotsam were inferred by examining the average distribution of flotsam-associated sets and consideration of the average surface circulation.

Two methods may be used to determine if different set types are related: correlation of set types occurring in an area and comparison of fork length distributions (length-frequency graphs) stratified by species and set type. Spearman's rank correlation coefficient (Siegel 1956) was calculated to expose possible correlations of numbers of sets. Fork length distributions were weighted by the catch in each set. A high positive correlation between set types occurring in an area would indicate a relationship between set types. Similar looking length-frequency distributions would serve as further evidence that set types are related.

An increase in the percentage of flotsam-associated sets would be evidence that flotsam-associated sets have become more important to the fishery. The CYRA was subdivided into three nearshore areas and one offshore area (Figure 1). Stratifying the number of flotsam-associated sets by area allows the determination of area effects. Hence, the importance of flotsam to the fishing industry may be determined by the percentage of flotsam-associated sets occurring each year and stratifying the number of flotsam-associated sets by area.

Average rainfall was tabulated to determine if any connection existed between river runoff and the number of flotsam-associated sets.

Catch rate is an indicator of the importance of flotsam-associated sets to the tuna fishery. Calculation of the average yearly catch per set (including zero catch sets) for different set types should

demonstrate any trends as well as the relative value of making one set type over another.

Calkins (1965) examined tuna length distributions from single sets in the eastern tropical Pacific, finding that single unassociated schoolfish sets caught tuna of a relatively uniform size (i.e., small variance in length). If the fish caught in flotsam-associated sets represent aggregations of solitary tuna, portions of schools, or several schools, then one would expect the variance of tuna length to be greater than for unassociated schools. In order to examine if floating objects act as aggregators, length-frequency data were stratified by species and set type. Mean length and standard deviation were calculated on a single set basis for each category and compared using Kruskal-Wallis one-way analysis of variance by ranks (Siegel 1956).

If flotsam does aggregate tuna, one would expect more of the larger flotsam-associated sets than unassociated sets. Differences in catch distribution were observed by plotting histograms of tons of tuna caught per set stratified by year and set type and by calculating catch per successful set for each year and set type. The single set catch data, collected by SWFC technicians, existed for the 1974-76 period.

RESULTS

The availability of logs or other flotsam in an area are determined by the source of the flotsam and the currents in the area. Large rivers flow into the Pacific from southern Mexico (lat. 20°N) and continue down the coast of South America (to lat. 20°S). These rivers are capable of releasing many logs into the Pacific during the rainy season. SWFC and IATTC observers reported large densities of logs near the Gulf of Tehuantepec (lat. 16°N, long. 100°W), the Gulf of Nicoya (lat. 10°N, long. 85°W), and the Gulf of Fonseca (lat. 13°N, long. 87°W).

The average yearly number of flotsam-associated sets in 1972-75 were plotted by 5° squares (Figure 1). In general, most flotsam-associated sets occurred in Areas 1 and 2. Most of the offshore flotsam-associated sets (i.e., Area 4) occurred quite close to Areas 1 and 2. Area 3 did not have large numbers of flotsam-associated sets. If the main source of logs and other flotsam is the rivers of Central America, then it is important to examine the major current patterns in the eastern tropical Pacific to determine if the currents can

explain the observed distribution of flotsam-associated sets.

The average currents in the eastern tropical Pacific, as derived from ship's drift data, were determined by Wyrski (1965). From January until May, the California Current is strong. Circulation near Area 3 is to the south. Circulation near Areas 1 and 2 is gyral. From May to July, both the Equatorial Countercurrent and the California Current are relatively strong. During this period, most countercurrent water turns north and flows along the coast of Central America. Area 3 has a northern and southern flow, the northern flow along the coast. Area 1 maintains its gyral flow. From August through December, the Equatorial Countercurrent is well developed. Circulation in Area 3 is to the south. Area 2 maintains its northwestern flow along the coast and Area 1 flow maintains a gyral pattern. If logs disperse mainly from the Gulf of Nicoya, the Gulf of Tehuantepec, and the Gulf of Fonseca, then the gyral circulation in Area 1 would tend to maintain logs and other flotsam in the area for a considerable time. The northwest coastal current in Area 2 could transport flotsam through Area 2 and during part of the year into Area 3. Since the North Equatorial and South Equatorial Currents are rather strong, one would not expect floating objects to persist in Area 4 except near the boundaries with Areas 1 and 2. Hence the location of large rivers and the system of currents is reasonably consistent with the geographical distribution of flotsam-associated sets.

In order to compare different set types, Spearman's rank correlation coefficient was calculated. For each 5° square in the CYRA, the total numbers of flotsam-associated sets, porpoise-associated sets, and unassociated schoolfish sets were tabulated for each year. These totals were ranked and the ranks were correlated. Only 5° squares where at least 10 sets occurred were used in calculating correlations. When a minimum of 40 sets was used as the criterion for including a 5° square, the correlations were qualitatively the same as with the 10 sets criterion. The results (Table 3) show that a significant positive correlation exists between number of sets on unassociated schoolfish and flotsam-associated tuna. Porpoise sets were uncorrelated with other set types.

The above results indicate that fish caught associated with flotsam tended to be caught in the same area at the same time as unassociated school fish. Examination of available length-frequency data on a species basis, weighted by the catch in

TABLE 3.—Spearman's rank correlation between three types of sets by year. Number of sets/5° square. (Source of data: IATTC.)

Year	N	Unassociated schoolfish and porpoise-associated	Unassociated schoolfish and flotsam-associated	Porpoise and flotsam-associated
1963	29	-0.0008	0.5421**	0.2538
1964	27	0.0375	0.1581	0.8138**
1965	25	-0.1597	0.3498*	0.1318
1966	28	-0.1110	0.3513*	0.2914
1967	24	-9.2379	0.4621*	-0.2255
1968	24	-0.1951	0.1886	0.3463*
1969	25	-0.1523	0.5957**	0.2294
1970	27	-0.0088	0.3529*	-0.0173
1971	26	0.0803	0.5819**	0.2398
1972	32	-0.0200	0.5277**	-0.0558
1973	34	0.0523	0.3086*	0.1796
1974	27	0.0168	0.4847**	0.0001
1975	33	0.2444	0.5139**	0.0526

*Significant at $P \leq 0.05$.

**Significant at $P \leq 0.01$.

each set (Figure 3), indicated that unassociated schoolfish and flotsam-associated yellowfin and skipjack tuna had very similar length-frequency distributions. The length-frequency information and the correlation analysis support the idea that unassociated tuna and flotsam-associated tuna are related. Flotsam, acting as an attractant, may aggregate tuna that would otherwise be caught in unassociated sets.

The number of flotsam-associated sets has increased dramatically since 1971 (Figure 2). The trend in percentage of flotsam-associated sets (Figure 4) indicates that flotsam-associated sets have increased in importance to the fishery. Stratifying the number of unregulated flotsam-associated sets by area (Figure 5) shows that the trend of more flotsam-associated sets is not an area effect. All areas, except Area 3, have shown a marked increase in number of flotsam-associated sets. Area 3 does not show an increase because logs are only deposited in this region during a limited portion of the year. In January-May, the near surface current in Area 3 is to the south (Wyrski 1965), cutting off the source of logs that wash down the rivers of Central America. Also, good fishing often occurs in Area 3 during the later months of the year, a period not included in my unregulated data. It appears that the increase in flotsam-associated sets in recent years was not caused by discovery of new areas with abundant flotsam but rather by an increase in fishing effort on flotsam in all areas but Area 3.

Average rainfall in Central America was tabulated (Table 4) to see if there was a correlation between river runoff and the number of flotsam-associated sets. Comparison of number of flotsam-associated sets and rainfall revealed only

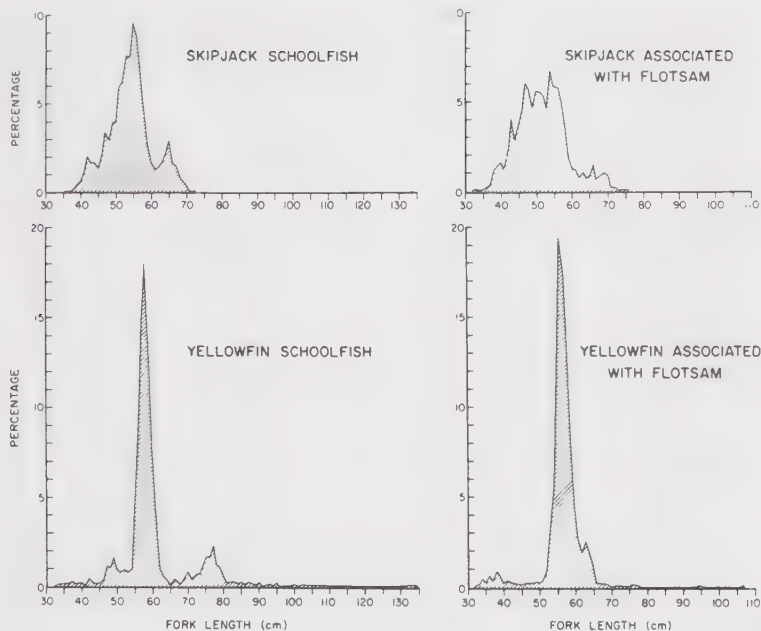


FIGURE 3.—Length-frequency distributions of yellowfin and skipjack tuna caught in unassociated schoolfish and flotsam-associated sets. Data collected 1973-75 in the CYRA (see Table 2).

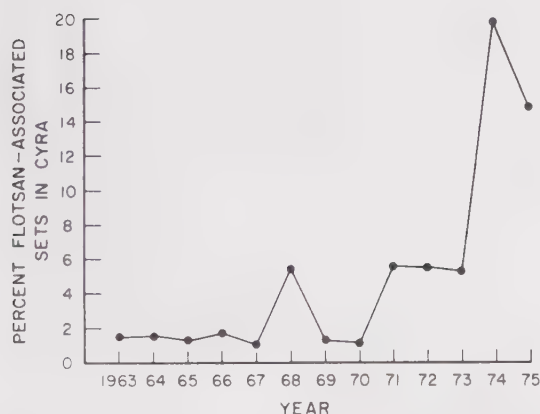


FIGURE 4.—Percentage of total unregulated sets that were associated with flotsam in the CYRA, 1963-75.

small similarities, indicating that the supply of suitable flotsam was not greatly influenced by rainfall.

Comparing the average catch per set of different set types indicates the relative importance of each set type to the fishery as well as showing trends in the catch rate (Figure 6). All set types had similar catch rates in 1963-66. Porpoise sets and flotsam-associated sets gave much higher catch per set than unassociated sets in 1971-75. One sees that flotsam-associated sets have been the most valuable set type for the tuna fisherman since 1971.

TABLE 4.—Average yearly rainfall (centimeters) in Central America in 1963-75. (Source: U.S. Department of Commerce.)

Average yearly rainfall		Average yearly rainfall	
Year		Year	
1963	139.0	1970	163.8
1964	136.4	1971	145.5
1965	136.9	1972	145.6
1966	158.5	1973	161.4
1967	151.7	1974	172.3
1968	177.3	1975	151.0
1969	177.2		

Fork length data was stratified by set type and species. The mean length, standard deviation, and sample size were calculated on a single set basis (Table 5). The average standard deviation of fork length of yellowfin and skipjack tuna associated with flotsam was larger than the standard deviation found in unassociated sets, though the mean fork length of flotsam-associated sets was smaller. The probability of getting the results shown (Table 5) by chance was calculated using Kruskal-Wallis one-way analysis of variance (Siegel 1956:184) (Table 5). The greater variability of fork length of flotsam-associated tuna supports the hypothesis that flotsam aggregates tuna.

The yellowfin and skipjack tuna catch distribution on flotsam-associated sets was compared with unassociated schoolfish sets. The average catch per successful set was calculated and the data were plotted as histograms of tonnages using an arbitrary interval of 5 tons (Figure 7). The main

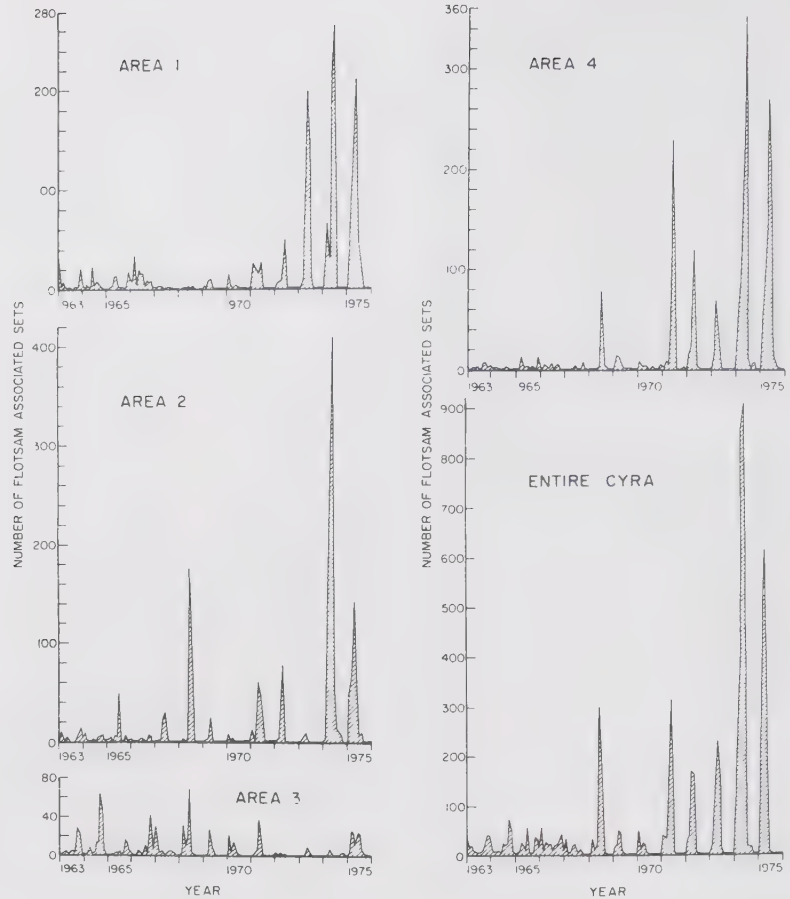


FIGURE 5.—Number of unregulated flotsam-associated sets per month by area, 1963-75.

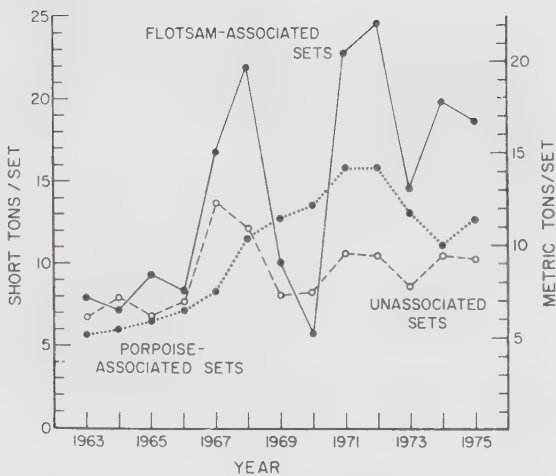


FIGURE 6.—Average yearly catch per set of yellowfin and skipjack tuna in flotsam-associated, unassociated schoolfish, and porpoise-associated sets in the CYRA.

differences between the histograms for unassociated schoolfish sets and flotsam-associated sets are a lower proportion of unsuccessful sets and a higher percentage of flotsam-associated sets with catches between 25 and about 60 tons. The higher proportion of large flotsam-associated sets is consistent with the hypothesis that flotsam aggregates tuna.

DISCUSSION

Changes in catch rate (catch per set, Figure 6) of flotsam-associated yellowfin or skipjack tuna may be related to overall abundance of flotsam-associated schools, technological advances such as bigger nets, increased skill and knowledge of the fishermen, changes of the attractability of flotsam, and changes in the residence time of tuna with flotsam. In order to explain the observed increase

TABLE 5.—Variability of fork length (centimeters) in single set data by tuna species and set type, as indicated by average standard deviation ($\bar{S}$) and mean ($\bar{x}$) and results of Kruskal-Wallis one-way analysis of variance of standard deviations. (Source of data: SWFC.)

Item	Yellowfin tuna	Skipjack tuna
Flotsam-associated sets:		
N	35	45
$\bar{S}$	4.96	4.62
$\bar{x}$	55.55	52.49
Unassociated schoolfish:		
N	49	43
$\bar{S}$	3.76	3.40
$\bar{x}$	60.94	54.08
Kruskal-Wallis:		
H	3.69	33.31
df	1	1
Probability level	$0.05 \leq P \leq 0.1$	$P \leq 0.001$

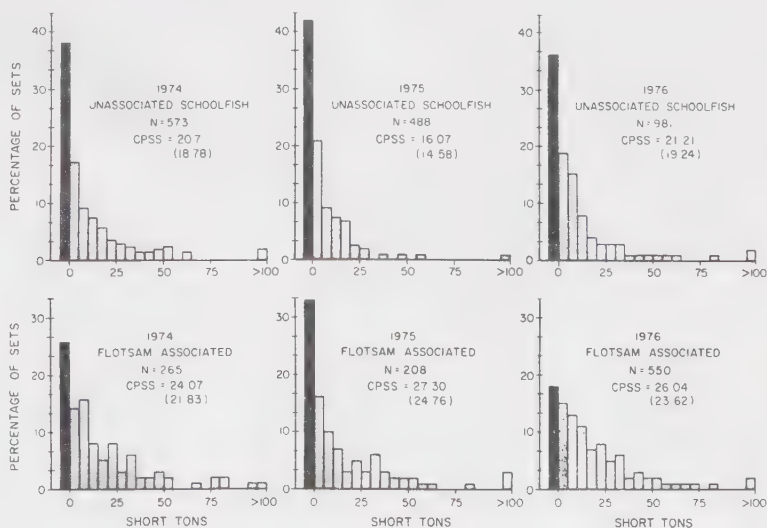
in catch rate, it was necessary to examine data that could indicate which factors have most influenced catch rate. Changes in attractability, changes in residence time, technological advances, and increased knowledge of the fisherman could not be rejected or confirmed with existing data. It was possible, with some assumptions, to determine if overall abundance changes or increased skill of the fisherman could explain the increased catch rate.

If the overall abundance of tuna had increased from 1963 to 1975, then one would expect the catch rate to have increased correspondingly. If one accepts the supposition that flotsam-associated fish were from the same population as unassociated schoolfish, then one would expect the catch rate on unassociated schoolfish to have likewise increased. The catch per set on unassociated schoolfish (Figure 6) showed no increase. How-

ever, the year-to-year variations in catch per set of flotsam-associated tuna and unassociated tuna (Figure 6) were remarkably similar. The above evidence indicates that changes in overall abundance does not explain the long-term increase of catch per set in flotsam-associated sets. The similarity of the year-to-year variations supports the hypothesized relationship between unassociated schoolfish and flotsam-associated tuna. The year-to-year variation may represent changes of abundance.

The second explanation for the changes in the catch rate of flotsam-associated tuna schools, changes in the skill of the fisherman, can be evaluated by the percentage of successful sets. An increase in the percentage of successful sets on schools associated with flotsam would explain the apparent increase in catch per set. Such an explanation is untenable because the percentage of successful sets would have had to more than double. Greenblatt (1977) calculated the percentage of successful sets associated with flotsam for 1974-76, finding the average percentage of successful sets to be 75%. To account for the change in catch/set, the percentage of successful sets in 1963 would have had to have been about 35%, an unreasonably low figure. Pella and Psaropoulos (1975, fig. 2) showed that the percentage of successful sets of unassociated schoolfish sets and flotsam-associated sets (considered as one category) did not increase enough in 1961-71 to account for the observed changes in catch per set. Bayliff and Orange (1967) reported percentages of successful sets stratified by set type for a limited area of the

FIGURE 7.—Distribution of catch by 5 short ton intervals for flotsam-associated sets and unassociated schoolfish from 1974 through 1976. Solid boxes indicate percentage of zero catch sets. The average catch per successful set (CPSS) in short and metric tons is given for each category. Metric tons are in parentheses.



CYRA. Although they had small numbers of sets, the percentage of successful flotsam-associated sets from 1962 to 1966 was 67.6%. Changes in percentage of successful sets can not adequately explain the increased catch per set.

No satisfactory explanation for the increase in catch per flotsam-associated set has been found. Overall increases in abundance or increased skill of the fishermen can not explain the increase. The above factors may account for some of the increase. Technological advances may account for the increased catch rate. It is also reasonable to believe that fishermen have learned to catch flotsam-associated tuna more efficiently and the residence time of tuna with flotsam has increased since 1967.

Changes in catch per set on flotsam-associated sets may have been due to technological advances such as bigger nets. If technological advances can explain the increased catch per set on flotsam, then either the catch per set on unassociated schoolfish should have also increased or sets associated with flotsam prior to the technological advances must have caught a low proportion of potential catch. Nets have increased in size, perhaps increasing the probability of catching yellowfin and skipjack tuna which may aggregate around flotsam. It is possible that bigger nets could account for increased catch/set of flotsam-associated sets without likewise affecting catch/set on unassociated schoolfish sets.

Fishermen often will drift with logs for considerable time, waiting for tuna aggregations to reach an optimal size before setting the net. The spread of such behavior throughout the fleet could cause the overall catch per set of flotsam-associated tuna to increase. Adequate data for testing this "increased knowledge" hypothesis was unavailable.

The marked changes occurring in flotsam-associated tuna catch in 1963-75 coincided with a large increase of effort and technology in the porpoise-associated fishery (Green et al. 1971). It is hypothesized that the increased effort and technology in the porpoise-associated fishery may have been related to changes in the catch rate of tuna schools associated with flotsam.

When purse seiners set on porpoise, there is often an incidental kill of the marine mammals. Due to recent technological advances, the porpoise kill has been reduced, but in earlier years of the porpoise-associated fishery (the mid-1960's) porpoise mortality was higher (Southwest Fisheries

Center³). This incidental kill may have reduced the porpoise population. The porpoise-associated fishery first developed near shore and thus the nearshore porpoise stocks have been affected for a longer time than offshore stocks. One may reasonably speculate that, on a species basis, nearshore porpoise stocks have been affected more by incidental kills than offshore porpoise stocks.

The bond between tuna and porpoise is not understood. It is possible that the mechanisms involved in the association of tuna with porpoise is similar to those responsible for their association with flotsam. Tuna associated with flotsam are, on the average, smaller than tuna associated with porpoise (Calkins 1965, tables 2 and 9; Sharp⁴). Knudsen (1977) gave some evidence that tuna caught in areas where porpoise fishing predominates were generally older and larger than in traditional schoolfish areas. Size overlap, however, did occur (Calkins 1965). Assuming that the number of porpoise schools have declined, the probability of tuna encountering porpoise schools has decreased. The probability of tuna aggregated near flotsam encountering porpoise schools has also decreased. Thus, as a result of decreased encounter rates with porpoise (slower transition from flotsam to porpoise), the size of the aggregations of tuna near flotsam have increased.

In conclusion, the most likely sources of flotsam are the large rivers of Central America. Indirect evidence indicates that tuna caught in unassociated schoolfish sets are from the same population as tuna caught associated with flotsam. It appears that the increase of flotsam-associated sets from 1963 to 1975 was due to an increased interest by fishermen and hence an increased fishing effort on floating objects. The observed increase in catch per set may have been a biological change rather than a change in fishing technology or skill.

ACKNOWLEDGMENTS

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³Southwest Fisheries Center. 1976. Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Tropical Pacific Yellowfin Tuna Fishery. SWFC Adm. Rep. LJ-76-29, 54 p. Southwest Fisheries Center, La Jolla, CA 92038.

⁴G. Sharp, Inter-American Tropical Tuna Commission, Southwest Fisheries Center, La Jolla, CA 92038, pers. commun. April 1977.

ful. Richard McNeely first suggested the possible interaction of porpoise and flotsam-associated tuna. The Inter-American Tropical Tuna Commission provided much of the data. William Flerx and Richard Charter provided insight into the operation of the fishery. Gary Sharp provided useful information about yellowfin tuna. Rainfall data were obtained from Eric Forsbergh. William Lenarz, Douglas Chapman, and Robin Allen reviewed the paper and offered constructive comments.

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SEASONAL DISTRIBUTIONS OF EPIPELAGIC FISH SCHOOLS AND FISH BIOMASS OVER PORTIONS OF THE CALIFORNIA CURRENT REGION

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ABSTRACT

Coarse distribution patterns of epipelagic fish schools over portions of the CalCOFI survey patterns are contrasted with estimates of biomass distribution patterns by season. Frequency distributions of fish-school sizes and peak target strengths are presented as well as the seasonal dependence in the position of these distributions. The data were collected on a series of six CalCOFI cruises during late 1974 and 1975.

INTRODUCTION

Sonar mapping yields rapid and efficient estimates of the numbers of epipelagic fish schools per unit area searched (Smith 1970; Mais 1974; Hewitt et al. 1976; Hewitt 1976; Fiedler 1978; Smith 1978). Estimates of mean school size are also possible and have been used to calculate the distribution pattern and abundance of schooled northern anchovy (*Engraulis mordax*) off the Californias (Mais 1974). Target strength measurements (indexing the ability of a school to reflect acoustic energy) have been made (Hewitt et al. 1976), but as yet an adequate understanding of the interaction between a pulse of sound and a dynamic array of scatterers does not exist to effect the incorporation of this parameter into an algorithm for the calculation of school biomass. On the other hand, fish distribution patterns inferred from the distribution of fish schools may be very misleading, i.e. it is not only possible but probable that a disproportionately large number of fish are in a small fraction of the schools.

This report compares coarse distribution patterns of fish based on pooled counts of schools per unit area surveyed and that based on school biomass estimates, assuming the schools were all of northern anchovy. The data used were from that portion of the 1975 ichthyoplankton surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) conducted by the R/V *David Starr Jordan*.

METHOD

The primary objective of the CalCOFI survey cruises was to observe hydrographic and plankton tow stations. The station pattern is typically of lines 40 miles apart, approximately at right angles to the coast, and stations

20 to 40 miles apart along the lines. Also, during the 1975 cruises there was an intensification of station density in the Los Angeles Bight. On the other hand, our acoustic sampling technique requires that the ship be underway. Further, in an effort to avoid the unknown effects on schooling and detection of schools at night and twilight, we operated the equipment only between the hours of 0800 and 1600 (Smith 1970). These conditions contribute to a less-than-optimum design for a plankton survey cruise. However, survey design was not the primary concern; our motivation was the opportunity to collect sufficiently large amounts of data to allow us to further investigate and quantify sampling bases.

Figure 1 describes the transect coverage for all six cruises. There is some overlap between cruises; but the portion of the CalCOFI grid that was surveyed is clear.

Figure 2 is a schematic description of the survey configuration. A 30 kHz narrow beam sonar (10° between -3dB downpoints) was directed at 90° from the ship's heading. The transducer was tilted down from the horizontal by 3° and transmitted 10 m sec pulses at 1-second intervals. The received signal was digitized at an interval corresponding to 1-m range and processed. Data recorded for each target included the time of detection, the mid-range of the target, the target size measured on a horizontal axis perpendicular to the ship's track, the peak target strength, and the number of sonar pings during which the target echo was detected (see Hewitt et al. 1976 for specific methodology). The ship's speed was also digitized and fed into the data processor, which interrupted data collection as the ship slowed to a stop and resumed data collection as the speed increased above a critical value. In this manner, acoustic data were collected along transects between CalCOFI stations. The range extent of the observation band was 250m—i.e. 200 to 450 m from the ship. Data from approximately 10,500 targets were logged during the six CalCOFI survey cruises.

RESULTS

Figure 3 describes the overall target size distribution for all cruises. The modal target size is about 45 m, and 50% of the targets are less than 50 m in size. The shape and position of this distribution is consistent with our

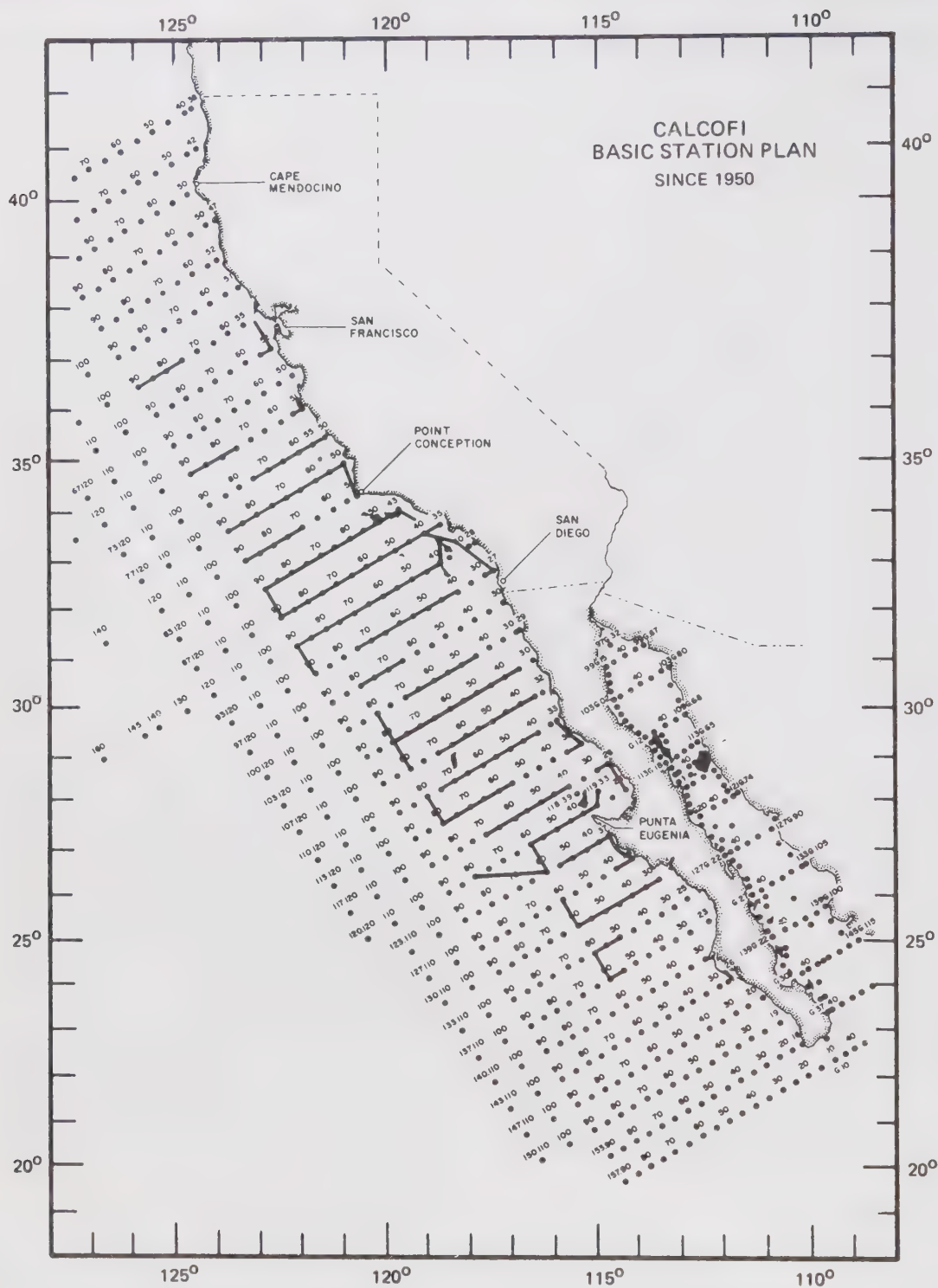


Figure 1. CalCOFI station pattern with sonar transect coverage for all cruises (from Vent et al. 1976).

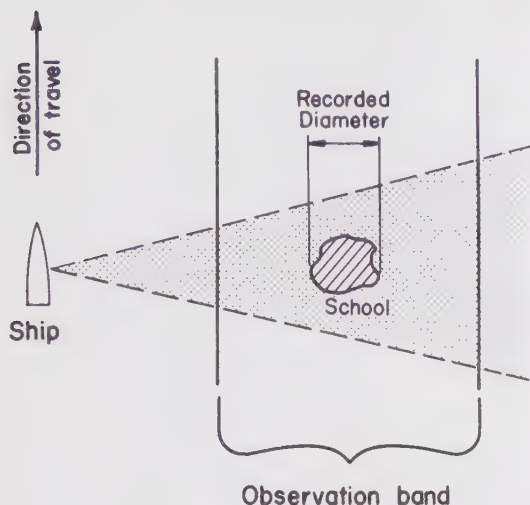


Figure 2. Plan view of the survey configuration

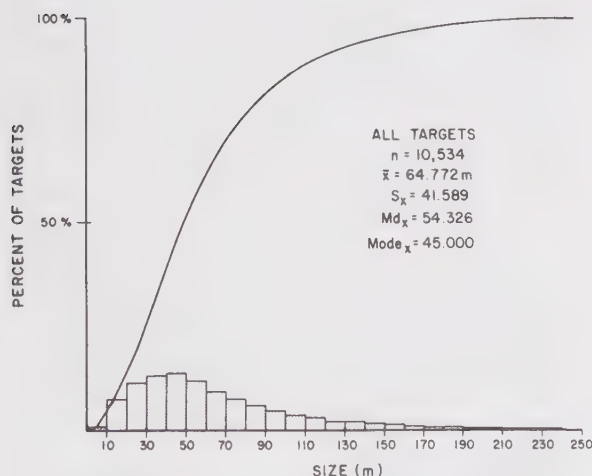


Figure 3. Overall target size distribution with descriptive statistics

previous experience.

Figure 4 describes the overall target strength distribution for all cruises. Here echo intensity is expressed in decibels, and the resulting distribution does not appear to be markedly skewed. The geometric mean of the power distribution is -7.8 dB and coincides with the modal target strength.

Figures 5 and 6 describe the variation of these values throughout the year. Target size was at a peak in the winter and declined steadily to a minimum in October 1975. Target strength appeared to peak in early winter and again in midsummer.

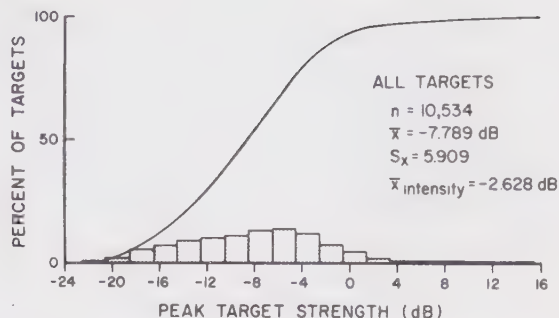


Figure 4. Overall peak target strength distribution with descriptive statistics

where $\bar{x} = \frac{1}{n} \sum_{i=1}^n TS_i$ and $\bar{x}_{intensity} = 10 \log \left(\frac{1}{n} \sum_{i=1}^n \text{antilog} \left(\frac{TS_i}{10} \right) \right)$, i.e. the geometric and arithmetic means of the power distribution

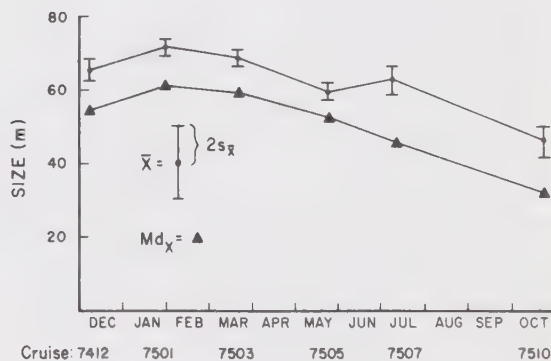


Figure 5. Seasonal variation of target size (1974-75)

DISCUSSION

The major importance of target size and target strength measurements to a stock assessment technique is the contribution these values make to an estimate of the fish biomass in an individual school. The biomass model, developed below, involves several assumptions at each stage of its development.

First is the characterization of the echo received from an array of scatterers. Weston (1967) has addressed this problem by dividing the return into two components: a coherent component reflected from the boundary of a fish school and an incoherent component reflected by individual fish. Weston further showed that at frequencies far above resonance, the coherent component becomes negligible and the target strength of an array is the summation of the contribution of individual scatterers adjusted for the effects of multiple scattering and attenuation within the sample volume.

Resonance frequencies for the two dominant epipel-

agic schooling species in the survey area, *Trachurus symmetricus* (jack mackerel) and *Engraulis mordax* (northern anchovy), have been reported to be near 1 kHz (Batzler and Pickwell 1970; Holliday 1972), which is well below the sonar operating frequency of 30 kHz. Thus, assuming only incoherent scattering, the acoustic scattering cross sections of n individuals within the sample volume are summed to equal the school target strength (TS):

$$(TS)_{\text{school}} = (TS)_{\text{indiv}} + 10 \log n$$

and

$$n = 10 \left(\frac{TS_s - TS_i}{10} \right) \quad (1)$$

We have assumed: 1) no multiple scattering of sound between fish or within the body of a single fish, and 2) negligible shadowing and attenuation of sound within the ensonified portion of the fish school. There is some support for this assumption from a Norwegian group (Røttingen 1976) who have measured a linear relationship between reflected acoustic energy and fish density over a moderate range of densities. It must be emphasized that this approach is a simplification, but a more rigorous model is premature. Using the present model, n may be expressed as a function of the school target strength and the target strength of an individual scatterer. However n represents the number of fish in the sample volume and not necessarily the entire school.

The sample volume is described in Figure 7 and may be approximated as the product of the x , y , and z dimensions. The x dimension is the range from which sound is received at any one instant; since we used an active sonar, we must account for a 2-way path and a pulse train of finite length. The z dimension is the vertical extent of the school; Mais (1974) has reported that we may expect considerably less variation in the vertical extent of fish schools as compared to their horizontal extent.

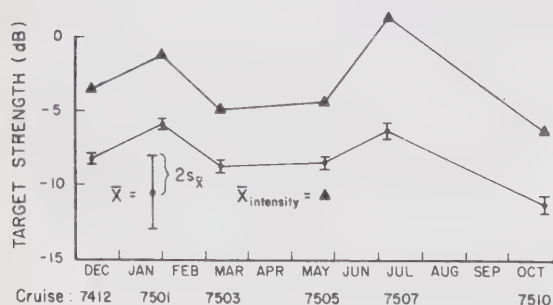
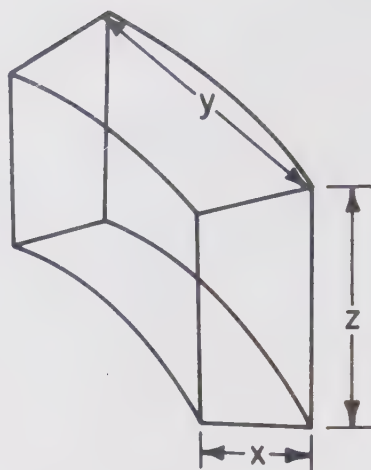


Figure 6. Seasonal variation of target strength (1974-75).



Where: $x = \frac{c\tau}{2} = \frac{1}{2}$ pulse length

$$y = 2R \tan \beta \quad \left. \begin{array}{l} \text{or } (D_H) \end{array} \right\} \begin{array}{l} \text{Whichever} \\ \text{is less} \end{array}$$

$$z = D_V$$

Figure 7. Estimation of the sample volume

The y dimension is limited by beam geometry or by the size of the school if less than the horizontal beam width at the range of detection. In determining the value of y , we have used the target range extent (school dimension as an axis perpendicular to the ship's track) as an estimate of the school dimension on an axis parallel to the ship's track.

With respect to the estimation of the sample volume, we have assumed 1) the horizontal profiles of the schools are elliptical and randomly oriented, i.e. as more targets are measured during a survey, the error introduced by measuring one dimension becomes negligible; and 2) the vertical extent of fish schools in the upper mixed layer is entirely ensonified by the sonar beam. The former assumption apparently leads to a systematic overestimate (Squire 1978), and the latter may lead to an underestimate.

The sample volume is estimated as a product of x , y , and z . Thus, where the sample volume is limited by school size:

$$V = \frac{c\tau}{2} (D_H) (D_V) \quad (2)$$

and where the volume is limited by beam geometry:

$$V = \frac{c\tau}{2} (2R \tan \beta) (D_V) \quad (3)$$

where c is the speed of sound through water, τ is the pulse duration and $c\tau/2$ is one-half of the pulse length in m, D_V is the vertical extent of the fish school, D_H is the horizontal school size, R is the range of detection, β is the half beam angle and V is the sample volume in m^3 .

The school biomass is estimated by applying the measured fish density to the entire school. The school shape is approximated by a cylinder of D_H diameter and D_V length. Thus,

$$B = \frac{n}{V} \left(\frac{\pi}{4} D_H^2 \right) (D_V) (W_i) \quad (4)$$

where B is the estimated school biomass and W_i is the weight of an individual fish.

At this point we have assumed 1) that the sample volume which yields the peak target strength is representative of the entire school, i.e. fish compaction is homogeneous throughout the school; and 2) that only fish of a similar weight are found within a single school.

By substituting equations (1), (2), and (3) into equation (4), two equations for the biomass of a school may be obtained that correspond to the limiting condition of the sample volume. For the case where sample volume is limited by school size

$$B = (k) 10^{(0.1 TS_s - 0.1 TS_i)} (D_H) (W_i) \quad (5)$$

and where the sample volume is limited by beam geometry

$$B = (k') 10^{(0.1 TS_s - 0.1 TS_i)} (D_H)^2 (W_i) (R)^{-1} \quad (6)$$

where k and k' are lumped constants. The school biomass may be thus expressed as a function of two measured variables: D_H (school size) and TS_s (peak school target strength) and two parameters that are specific to the species under study: W_i (weight of an individual) and TS_i (target strength of an individual). As a final note, D_H is reduced by one-half the pulse length ($c\tau/2$) to counter the increase in apparent range extent that occurs when a pulse train of finite length is used.

An idea of the sensitivity of the biomass estimate to assumed values for W_i and TS_i may be obtained by estimating the biomass of the most commonly observed school in terms of size and target strength (45 m, -7 dB) for various values of W_i and TS_i . for this purpose we will assume that the sample volume is limited by the school size. From an examination of Table 1, it is clear that the biomass estimate is much more sensitive to TS_i than W_i . As may be expected from an examination of equation (5), the biomass estimate changes in direct pro-

portion to W_i and by an order of magnitude for every 10 dB change in TS_i .

TABLE 1
Estimated Biomass (in metric tons).

W_i (in g)	TS_i (in dB)				
	-40	-45	-50	-55	-60
12	0.09	0.30	0.94	2.97	9.40
13	0.12	0.37	1.18	3.72	11.75
18	0.14	0.45	1.41	4.46	14.10
21	0.16	0.52	1.65	5.20	16.45
24	0.19	0.59	1.88	5.95	18.80

Conceivably an areal distribution of fish that is based on target size and target strength might be considerably different than one that is based solely on target counts. To see this effect we assumed that all of the schools were composed of adult anchovy with an individual weight of 18 g and an individual target strength of -50 dB.

Figure 8 shows the biomass frequency distribution for all of the targets encountered during the 1975 CalCOFI surveys. Ninety percent of the schools are 5 tons or less, and only 1% are greater than 45 tons.

Figures 9 through 13 compare the geographic distribution of fish as indicated by the number of targets detected per km^2 and by metric tons per km^2 . It should be emphasized that these are coarse plots drawn from data points pooled over several 10's of km. As such, they are smoothed and do not represent the true contagion experienced in the distribution of fish schools.

Figure 9 was drawn from data collected in December 1974. The plot on the left describes the distribution of epipelagic fish schools in numbers per km^2 . The contour interval is one school per km^2 . Starting from Sebastian Viscaino Bay and proceeding northwest, there appears to be a monotonic increase in the numbers of schools per unit area. The plot on the right describes the distribution of estimated fish school biomass. Contour intervals are 5 metric tons per km^2 , and the distribution pattern appears to be quite similar to the school distribution.

Figure 10 is drawn from data collected in January 1975. Here the comparison is somewhat different. The number of schools per unit area appears to be increasing with distance offshore, whereas the estimated biomass per unit area appears to increase in a south-to-north direction.

Figure 11 is compiled from data taken on a survey in March 1975. Although there appears to be a moderate concentration of schools offshore, the estimated biomass distribution has little relief. The relatively high concentration of estimated fish biomass in Sebastian Viscaino Bay is in contradiction to the distribution trends of fish schools.

Figure 12 describes data taken in May 1975. There is

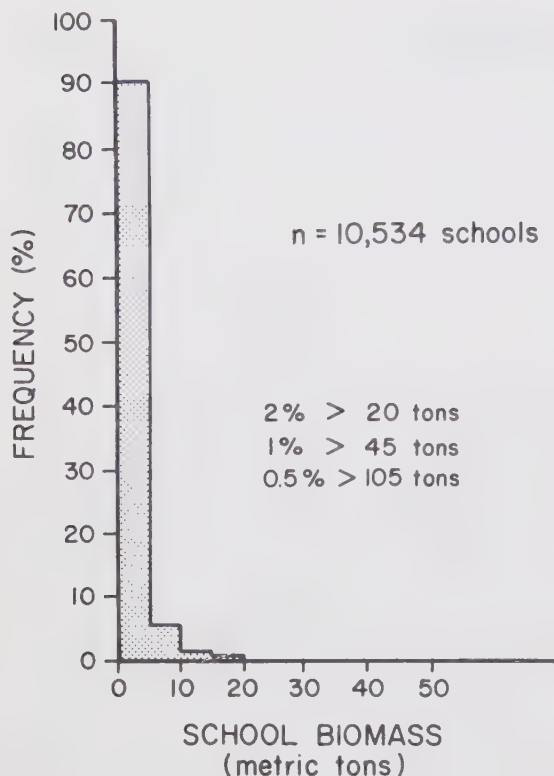


Figure 8 Overall distribution of estimated school biomass

a concentration of fish schools per unit area offshore of northern Baja California and relatively few schools in the Los Angeles Bight. However, the distribution of estimated biomass per unit area shows the highest concentration in the inshore portion of the Los Angeles Bight.

Figure 13 is from data taken on the July 1975 CalCOFI cruise. Here relatively few numbers of fish schools were estimated to contain a relatively large amount of fish biomass. The highest concentration of estimated biomass per unit area is inshore.

The October 1975 cruise was not plotted, because it was conducted over too small an area. If a simple integration of biomass per unit area over area surveyed were performed and then normalized to counter the effect of unequal survey effort, the results would show the highest estimates of biomass in the months of January 1975 and July 1975.

The message contained in these plots is clear: the distribution (and abundance) of a target species inferred from the density of schools per unit area may be seriously misleading. Admittedly, these are coarse plots based on a crude biomass model, but we believe that a more

sophisticated analysis, while certainly necessary, will not alter appreciably the basic results. It remains that a survey scheme that maps the occurrence of fish schools should acknowledge large between-school variations in fish packing density if it hopes to reproduce the distribution pattern of the fish.

A final note should be made of sampling biases, for which no attempt was made to correct but which we feel were constant enough so as not to change the qualitative results presented here. We have so far identified three major sources of systematic error; the first results from the use of a finite observation band where only those targets that lie entirely within the observation band are logged. As a consequence, large schools are undersampled relative to small ones because the range over which they may be detected is proportionately smaller. The second bias is caused by a range-dependent detection-rate loss, i.e. fewer targets are counted at longer ranges and the loss rate may vary seasonally and/or regionally. The third error arises from the fact that many schools are amoeboid-shaped (Squire 1978). By assuming school shape to be elliptical, we have overestimated the area of a school with any concave curvature of its perimeter. This effect may be examined with video tapes of school shapes taken with an airborne camera.

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Figure 9. Geographic distribution pattern of schools and estimated fish biomass detected during cruise 7412 (December 1974)



Figure 10. Geographic distribution pattern of schools and estimated fish biomass detected during cruise 7501 (January 1975)



Figure 11. Geographic distribution pattern of schools and estimated fish biomass detected during cruise 7503 (March 1975).



Figure 12. Geographic distribution pattern of schools and estimated fish biomass during cruise 7505 (May 1975).



Figure 13. Geographic distribution pattern of schools and estimated fish biomass detected during cruise 7507 (July 1976).

Interactions Between Piscivorous Fishes and Their Prey

Edmund S. Hobson

Most fishes that prey on other fishes face what might seem a simple enough task: they must run down, or otherwise capture, organisms that are smaller, and weaker, than they are. Generally, their attacks are direct approaches to exposed prey that are large enough to grasp, yet small enough to manipulate. And once ingested the prey are usually swallowed whole.

These predators are well built for the job. Fish-eaters, or piscivores, generally have large, but relatively simple mouths, and short uncomplicated digestive tracts. These features have remained relatively unchanged during a long period of evolution that has seen major alterations in the feeding mechanisms of species which forage on other kinds of aquatic organisms (see Gosline 1959, Hobson 1974). Obviously, they attack with proven equipment.

Nevertheless, despite the conservative nature of their feeding apparatus, and what might seem a straightforward predatory task, other parts of their anatomies, and also their feeding related behaviors, have diversified greatly to meet severe problems that stem from capturing prey. And the finely tuned interactions between these predators and their prey are further evidence of powerful evolutionary forces. Attacks by fish-eating predators during the evolution of modern species have pressured prey to acquire effective defensive adaptations. But every successful defense has in turn evoked an appropriate offense, so that a delicate balance now exists. The opposing forces that maintain this balance, as expressed in adaptations of both predators and prey, and the patterns of predation that have resulted, are the topics of this chapter.

I have developed a synthesis based on published reports that should have widespread

relevance even though most of the material draws from fishes in tropical and warm-temperate seas. These warmer marine habitats have proven most fruitful for study of the topics considered here, because feeding interactions among members of their exceptionally rich and diverse faunas exhibit especially well-defined patterns. This is largely because so many of the interacting species in these places have highly specialized feeding habits. It is one of the axioms of biology that interacting species become more specialized as their numbers increase. Nevertheless, the principles that emerge from this synthesis should apply even where species are fewer and less diverse, and where feeding patterns perhaps are less distinct.

Major Offenses of Piscivorous Fishes

Most fishes that prey on other fishes use one of four predatory strategies, each strongly reflected in the user's body features. They either (1) run down prey, (2) ambush prey, (3) habituate prey to an illusion that they are nonaggressive, or (4) stalk prey.

Predators that run down their prey are the most widespread because their major asset — speed — is particularly suited to the most widespread habitat — open water. They tend to be highly streamlined, with cylindrical, heavily muscled bodies and deeply forked tail-fins. The tunas (Scombridae) and the billfishes (Istiophoridae) are oceanic examples, whereas jacks (Carangidae) are prominent representatives in nearshore marine waters (Figure 1). The straightforward attacks that characterize these predators, however, are less effective in the confined spaces of shallow water and near the bottom, especially where prey are just a quick dart from

a sheltering reef or grass bed. Such circumstances favor predators that use one of the following three ways to catch prey.

Predators that ambush prey generally rest immobile on the bottom and capture organisms that have inadvertently come within range of a short, explosive charge. The color and texture of some, for example, certain scorpionfishes (*Scorpaenidae*), are similar to that of the substrate on which they lie, while others, like certain flatfishes (*Pleuronectiformes*), may rest under a layer of sand (Figure 2).

Some ambushers capture prey without leaving their position on the bottom. When prey approach closely to the Hawaiian scorpionfishes of the genus *Scorpaenopsis* (Figure 3), for example, these big predators simply snap open their cavernous mouths and gill cavities and suck their victims in (Hobson 1974). A few species have embellished the ambushing tactic by acquiring features that actively draw prey to them; thus, certain anglerfishes (*Antennariidae*) have a fin spine modified as a lure that attracts potential prey (Figure 3).

Predators that habituate prey to an illusion that they are nonaggressive, including certain basses (*Serranidae*) and snappers (*Lutjanidae*), often live side by side with their ultimate victims (Figure 4). Most are sluggish, sometimes large fish, but can explode upon prey with a burst of speed over short distances. These predators often hover above the bottom in full view, which distinguishes them from the ambushers. Generally, their coloration and demeanor render them inconspicuous, so they regularly go unnoticed, if not unseen. Their success as predators depends on prey becoming accustomed to their presence, lulled by their peaceful mien and ultimately careless.

Predators that stalk prey typically include long, attenuated fishes like barracudas (*Sphyraenidae*), pikes (*Esocidae*), needlefishes (*Belonidae*), and cornetfishes (*Fistulariidae*). By drifting forward slowly, showing overt aggression only when close upon an unwary victim, they arrive within striking range of their target despite being in full view. Many stalkers have exceptional feeding structures that are in contrast to the generalized equipment of most other fish-eaters. The cornetfishes (Figure 5), for example, have an exceptionally long, tubular snout, which, when suddenly expanded, sucks

in prey they have managed to approach.

The last three strategies cited are described in pure form. Although the examples given are highly distinctive, many piscivores, for example, certain sea basses, incorporate components of two, or even all three, of these strategies. Furthermore, some piscivores have adopted specialized variations of these strategies. The leather bass, *Dermatolepis dermatolepis* (Figure 6), for example, commonly gains predatory advantages by associating with both schools and individuals of other species. Sometimes the leather bass approaches prey from behind these other fishes, apparently using them as a blind to get within striking range unnoticed; other times the bass follows alongside herbivores and other grazing fishes and captures prey that are driven from cover as the grazers disturb the substrate. (Montgomery 1975).

Major Defenses of Prey

The strategies used by piscivorous predators are responses to the defenses of their prey. Major defenses include both behavioral and anatomical adaptations, and are used by most prey species in some combination. Schooling and staying within reach of shelter are important defensive behaviors, whereas spininess and body armor are important anatomical adaptations.

Virtually all small fishes school when they are away from a sheltering reef or other structure during the day, and almost invariably smaller species that spend all their time in open water school habitually. It is widely believed that fishes are protected from predators when they school, although opinions vary on how this occurs. Some suggest that when fishes school they reduce their encounters with predators (Brock and Riffenburg 1960, Olson 1964), whereas others believe that schools increase security because predators regard the group as some inedible, or threatening, object (Crawford and Powers 1953, Springer 1957).

Some note that the greater number of eyes and other sensory receptors in the group make it significantly more probable that a threatening predator will be recognized (Bowen 1931); others suggest that schools have resulted because individuals in the center are protected by those of their kind between themselves and the predators (Williams 1964, Hamilton 1971).

Any one of the above possibilities could be a factor under appropriate circumstances, but generally I favor the theory that advantage is gained through a "confusion effect" (as advocated by Allen 1920a, 1920b, Manteifel and Radakov 1961, Eibl-Eibesfeldt 1962, Hobson 1965, 1968, Starck and Davis, 1966, Neill and Cullen 1974).

The confusion effect theory contends, in essence, that predators confronted by the many targets in a school commonly fail to concentrate on an individual. Many characteristics of schools are understandable when considered as enhancing a confusion effect. Schooling fishes emphasize features that make individuals difficult to distinguish. Thus, all members of a school are about the same size and look much alike. Schooling fishes are noted for lacking external differences between the sexes. When threatened, schooling fishes typically close ranks, a maneuver that places additional individuals within the attacker's field of vision, thus further troubling those that have difficulty with multiple targets.

Schoolers under attack also swim faster and begin weaving in and out among one another, a maneuver that appears to increase the confusion effect. At this point the silvery hues that characterize so many schoolers come into play, as sunlight reflecting from their sides at rapidly changing angles would seem to present the attacker with a bewildering shower of brilliant flashes (Hobson 1968). Similarly, the bars or stripes that characterize the color patterns of many schoolers tend to blend together as a shifting maze of lines that conceal individuals (Starck 1966). And just as the protective aspect of the school requires its members to present a uniform appearance, it also requires them to present uniform behavior. Thus, it seems likely that any individual that swims abnormally, for example, because of injury, becomes a distinctive target (Hobson 1968).

Every successful defense in prey will be answered among predators by an appropriate offense. So it should be expected that some predators have solved the defensive features of schools. The sword of the swordfish (Xiphiidae) and the saw of the sawfish (Pristidae) may be effective weapons when attacking fish schools (Williams 1964), as may the long tail of the thresher shark (Alopiidae) (Nichols and Murphy

1916). But so long as the vast majority of fish-eating predators is frustrated by the defensive aspect of schools, their failures will cancel out the successes of the relatively few specialized forms that seem to have solved the problem.

The advantage of schooling as a protective device is unneeded by smaller fishes that live close to the sea floor, because these find shelter in or close to reefs and other structures. Some, like the razorfishes (Labridae, *Hemipteronotus* spp.) are specialized to dive into the sediments. Still others, like certain goatfishes (Mullidae), seem secure simply by being close to the substrate; perhaps their immediate proximity to the sea floor sufficiently inhibits the space-demanding attacks of predators that might otherwise threaten them, or perhaps they simply go unnoticed by most predators. In any event, as long as these various species are close to shelter many of them feed, and carry on other pursuits, as solitary individuals. Some of them, however, for example the damselfish *Abudefduf troschelii*, periodically swim up into midwaters, and at these times generally school with others of their kind (Hobson 1968).

Although small reef fishes face an intense threat from predators when they move away from shelter, some nevertheless spend their active hours in the midwaters. But even these are careful to stay within reach of shelter on the sea floor. Many such fishes, including various damselfishes (Pomacentridae, especially *Chromis* spp.) feed on zooplankton, and though they acquire a measure of security by aggregating, they nevertheless remain dependent on shelters that lie far below them. Significantly, most of these plankton-feeders, or planktivores, have acquired features that increase their swimming speed and thus hasten their descent to cover when threatened (Hobson 1974).

Compared to close relatives that spend all their time near the reef, these planktivores tend to have more cylindrical bodies and more deeply incised tailfins (Davis and Birdsong 1973) — two tendencies that increase their speed. Furthermore, these speed-inducing features are most pronounced in those species that habitually range farthest into open water (Hobson and Chess 1978). That they use this speed is demonstrated when certain predators appear — notably jacks — and the entire assemblage abruptly closes ranks and dives headlong toward the reef

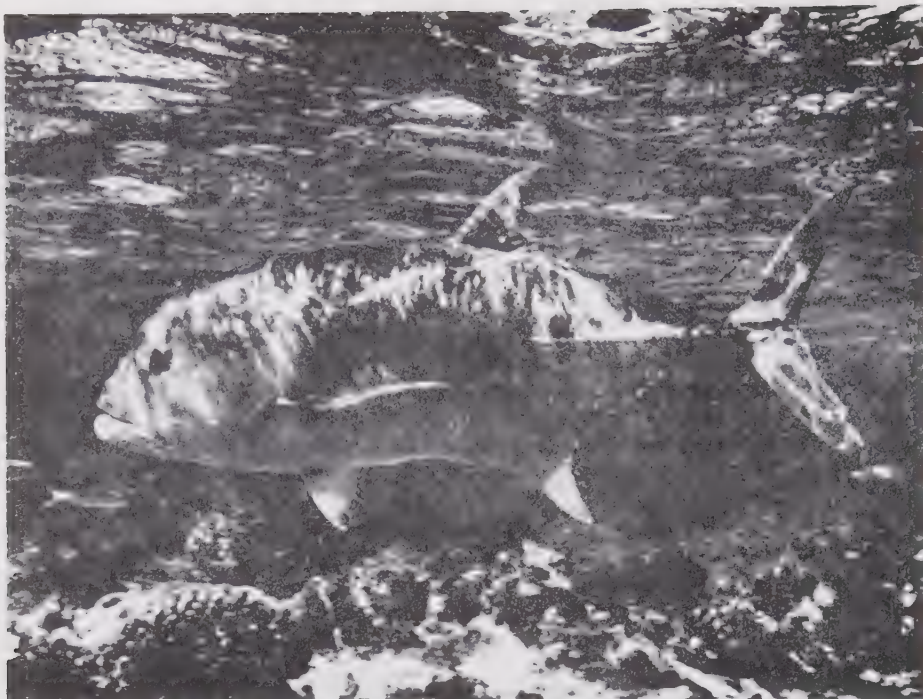


Figure 1. This large jack, *Caranx ignobilis*, here patrolling near shallow reefs at Midway Atoll, Hawaii, is built to run down prey with an aggressive, straightforward charge.



Figure 2. This California halibut, *Paralichthys californicus*, will erupt from its concealed position under the sand off the California coast to ambush small fishes that have come within range of a short, explosive charge.



Figure 3. With a sudden expansion of its cavernous mouth and gill cavities, this scorpionfish, *Scorpaenopsis* sp., sucks in prey without leaving its perch on this Hawaiian reef. The small, white appendage just inside its lower lip, which often is moving and highly visible while the fish rests motionless and otherwise virtually unseen, may lure prey to within range of capture.



Figure 4. Even though these large groupers, *Mycteroperca rosacea*, hover in full view above this reef in the Gulf of California, they nevertheless feed on the small fishes about them. Perhaps their sluggish countenance habituates prey to an illusion that they are nonaggressive, and ultimately the prey become fatally careless.



Figure 5. The long, attenuated body of this cornetfish, *Fistularia commersoni*, here gliding above a reef in the Gulf of California, accentuates features that characterize stalking predators.



Figure 6. A leather bass, *Dermatolepis dermatolepis*, amid a school of the chaetodontid *Heniochus nigrirostris* in the Gulf of California. This chaetodontid is not prey of *D. Dermatolepis*, but apparently the serranid enhances its chances of approaching unnoticed to within striking range of prey by mingling with these and other fishes.

below. Because there is a direct relation between swimming speed and body length, it is unsurprising that within a group of closely related planktivores the smaller species remain closest to cover; thus, the smallest of the Hawaiian planktivorous damselfishes, *Chromis vanderbilti*, rarely feeds more than 0.5 m above the reefs, whereas larger relatives, like *C. ovalis*, typically feed 2 to 5 m above (Hobson 1972, 1974, Munz and McFarland 1973).

Ultimately, even the most elusive prey will likely find itself between the jaws of a predator. But even from this position the attacker can be deterred. The strong fin-spines that characterize many fishes certainly complicate the predator's task. A predator that has successfully taken a relatively large spiny-finned fish into its mouth now must position the prey to enter its narrow digestive tract head-first. An attempt to swallow such prey tail-first would likely result in the spines locking erect and becoming lodged in the pharynx or esophagus. I have seen many predators fatally choked this way. Also, during the split second that the predator must relax its grasp for proper positioning, I have seen predators lose the prey fish they had held firmly between their jaws.

Spininess, like most successful defenses, is developed to extremes in some species, but these extremes generally limit other abilities. Thus, certain rockfishes, *Sebastes* spp., have large bony heads that carry many fixed spines, and surely present predators with a troublesome mouthful. But the added weight of these structures ties those that bear them to a largely sedentary life on the sea floor. Significantly, more motile rockfishes, like the olive rockfish, *Sebastes serranoides*, have smaller heads with fewer and less pronounced spines.

An effective combination of strong fin spines and exceptionally deep bodies probably protects butterflyfishes (Chaetodontidae) and angelfishes (Pomacanthidae) from most of the predators that threaten their neighbors on coral reefs (Hobson and Chave 1972). Furthermore, some reef fishes that habitually swim into the exposed midwaters and feed on plankton, for example, damselfishes of the genera *Dascyllus* and *Amblyglyphidodon*, have longer fin spines and much deeper bodies than do their relatives that remain close to sheltering reefs. Thus in response to the same predatory threat that has

led to more cylindrical bodies and deeply incised caudal fins in many other planktivorous damselfishes, the evolution of these species seems to have taken the opposite course. Where a cylindrical body (and deeply incised tail fin) promotes eluding predators, the deep body (with long fin spines) would seem to promote discouraging predators — two opposing routes to the same end: to reduce the threat of attack (Hobson and Chess 1978).

Patterns of Predation

Interactions between predator and prey are shaped by the way these animals perceive their surroundings. Their orienting senses, therefore, are presumably major elements in defining predation patterns. Clearly, most piscivorous fishes depend mainly on vision to capture prey. Despite notable exceptions, especially among species that frequent dark or turbid waters, the predominance of vision on a broad scale is unquestionable. Of course, the range of vision underwater is sharply limited. Light diminishes rapidly as it passes through even the clearest natural water because it is scattered by suspended particles and is absorbed by the water itself; consequently underwater objects no matter how large, are invisible beyond about 70 m (Brock and Riffenburg 1960). So predators must use some other sense to detect prey at greater distances.

Thus, certain sharks track injured or distressed fishes over long distances by orienting on odors characteristically emitted by these prey (as long as the odor trails out in a current, or behind moving prey). But even sharks drawn in by odors generally switch to visual cues when close to their target (Hobson 1963). So with visual ranges in the aquatic realm limited, the major interactions between predators and their prey are at close range — a set of circumstances that undoubtedly has contributed to most large predators being nearsighted (Walls 1942). And with visual orientation so important, feeding interactions are strongly influenced by the changes in underwater light that characterize the different times of the day-night cycle.

Because most piscivorous fishes orient visually when they feed, one might expect attacks to increase with the brightness of underwater light. By this reasoning, however, attacks

should be most frequent during midday, when in fact activity among predators is at a low ebb. Probably this mild paradox reflects a long, successful evolution that has given prey defenses that effectively counter the offensive strengths of their predators. If predators can see better in bright light, so can their prey, and the lack of activity among predators during midday suggests that during this period defense has an edge over offense.

Certain prey defenses, at least, are best suited to bright light. Features of the school that would enhance a confusion effect should be most effective under bright light. These features include flashing silver sides and color patterns consisting of bars or stripes. Even the confusion effect itself, which entails presenting the attacker a complex visual image, may increase or decrease with light. Whether or not this is so, schooling fishes appear relatively safe from predators during most of the day (Hobson 1968).

No matter how effective the daytime, or diurnal, defenses may be, however, there are bound to be lapses during which the prey are briefly vulnerable. For example, small fishes that ordinarily stay within reach of shelter will sometimes stray too far into the open, and others normally secure in schools will briefly separate from their group. Still others, usually alert to developing dangers, will be momentarily distracted. The most successful diurnal piscivores are those best able to exploit such defensive mistakes.

But prey are unlikely to make errors of this sort in the presence of jacks and other aggressive free-swimming predators. Prey recognize signs that mark hunting predators, and take appropriate action when aware that one is about. Those that find safety in the reef move toward these shelters, and those that are secure in schools tighten their ranks. Above all, the prey are alerted, so that few suitable targets are available to those predators that characteristically run down their prey with a highly overt, straightforward charge.

Of course, such predators enjoy occasional midday successes. Sometimes groups of jacks charge into schools of small fish, seemingly in a coordinated effort to scatter the school and thus isolate individuals (Eibl-Eibesfeldt 1962, Starck and Davis 1966). Using a different tactic, jacks and skipjacks (Scombridae) may accom-

pany schooling prey for hours without making an aggressive move, then suddenly attack (Hiatt and Brock 1948, Hobson 1968), presumably having sensed a vulnerable individual. But these are relatively infrequent successes; predators of this type remain better suited to hunt under other conditions.

Adaptations that place predators within striking range when smaller fishes become momentarily vulnerable during the day characterize the ambushers, those that habituate prey to their apparent nonaggressiveness, and the stalkers. Included here are most of the species that capture smaller fishes through the day on tropical marine reefs (Hobson 1974, 1975). Their closely related feeding strategies express a common goal: to catch prey unaware in a vulnerable position. That their most distinctive features seem designed to exploit relatively infrequent lapses in the defenses of their prey testifies strongly for the considerable strengths of these defenses.

If the major defenses of smaller fishes are most effective in daylight, what becomes of these fishes at night? It appears that after dark they are comparatively free of the intense threats from predators that so strongly influence their every move during the day. Predators that threaten smaller fishes on tropical marine reefs by day are largely inactive, or shift to some other prey, at night (Hobson 1968, 1973, 1974). This observation is true despite some fish-eaters that are specially equipped to capture their prey at night. One such predator is the big-eye jack, *Caranx marginatus*, a large fish whose name describes the distinctive feature that permits it to see better in the dark; it hunts smaller fishes at night in the eastern Pacific Ocean (Hobson 1968). But compared to the number of piscivores abroad in daylight, few are active at night.

Some of the smaller night-active, or nocturnal, predators that feed chiefly on crustaceans and other free-swimming invertebrates — including soldierfishes (*Myripristis* spp.), glass-eyes (*Priacanthus* spp.) and cardinalfishes (*Apogon* spp.) — take small fishes, especially larval forms, but only as a relatively minor part of their diets (Hiatt and Strasburg 1960, Randall 1967, Vivien 1973, Hobson 1974). Perhaps smaller fishes fail to generate the stimuli that orient nocturnal predators, or perhaps

they simply are too elusive to be caught consistently by most predators that feed in the dark.

The smaller fishes themselves offer evidence that at night they enjoy a sharply diminished threat from predators. The two major defensive behaviors that protect them by day — schooling and staying close to shelter — are greatly relaxed at night. Breder (1959) stated, "The dispersion of schools in darkness has been so often reported that it is to be expected unless otherwise shown." Although some fishes maintain their schools during the night, especially certain open-water species, generally the assemblages are much looser, and individuals are much farther apart.

Proximate shelter certainly becomes less critical at nightfall, as many species that stay close to reefs in daylight range into open regions after dark. Thus, the open sandy expanses adjacent to reefs in the Gulf of California are largely without visible signs of life during the day, but are transformed into centers of nocturnal activity as fishes flood from the reefs into these expanses at nightfall (Hobson 1965, 1968). Evidence of a diminished threat at night also exists among the body features of the smaller fishes. For example, the widespread tendencies among planktivorous reef fishes toward more cylindrical bodies and deeply incised tails — features that permit a speedier retreat to cover when threatened — occur only in species that feed in the midwaters by day. Features of this sort are lacking among nocturnal counterparts, including certain soldierfishes, and cardinalfishes (Hobson 1974, 1975).

So far I have described a system that would seem to favor the prey; they are well protected by effective defenses during most of the day and face only a relatively minor threat from predators at night. But conditions change drastically during the morning and evening transitions between day and night. Defenses effective in bright daylight falter as light diminishes, so that the transition periods, though relatively brief, provide many piscivorous fishes their major feeding successes.

Actually the balance begins to shift from prey to predator long before twilight. Even during midday, in fact, small fishes that are feeding on plankton in the midwaters descend closer to sheltering reefs whenever visibility is reduced. This descent occurs either with a drop in light, as when clouds pass before the sun, or through

a drop in water transparency, as when turbid water inundates an area (Hobson 1972, Stevenson 1972). Presumably this descent by the planktivores is in response to a measurably greater threat from predators that accompanies even slightly decreased visibility. As light continues to fade with the advancing afternoon, the planktivores descend progressively closer to the bottom — a descent that probably provides a rough index of increasing danger.

As day's end approaches, the fishes that had been active above many tropical reefs show a clear relation between their size and the time they go under cover. The smaller individuals, which are most vulnerable to predators, seek shelter first, and by sunset many of them already are out of sight (Hobson 1972). Many of the larger diurnal fishes, however, remain above the bottom for some time into twilight. Then, about 15 minutes after sunset, these too move from exposed positions, and the reef experiences what has become known as the "quiet period" (Hobson 1972, Munz and McFarland 1973, Major 1977).

It is during this "quiet period," a short span of about 20 minutes during both morning and evening twilight, that smaller fishes appear to be most vulnerable. The evening quiet period on tropical reefs is that time shortly after sunset when the day-active fishes have retired to shelter, but the night-active fishes have not yet emerged, and the morning quiet period is the comparable time shortly before sunrise when the sequence is reversed. The term quiet period, then, describes a general absence of fishes in exposed — and therefore vulnerable — locations. Although descriptive of most tropical reefs, the term clearly is a misnomer in reference to others. Where schooling fishes abound, this often is a time when large predators attack most intensely. The major attackers under these conditions are those aggressive piscivores like jacks whose feeding seems most inhibited during midday. Unlike so many other smaller fishes, the schoolers generally are unsuited to shelter in the reefs and so remain exposed to what obviously are precarious circumstances. Thus, the waters around herring (*Harengula*) schools in the Gulf of California (Hobson 1965, 1968), and silverside (*Pranesus*) schools in Hawaii (Major 1977), often are whipped into a frenzy of predatory activity at a time when

conditions appear tranquil elsewhere.

The end of the quiet period, about 35 minutes after sunset, is marked by a surge of nocturnal fishes, notably soldierfishes, that abruptly emerge from their daytime shelters, and swim straight away into the midwaters. The intense predation on schooling fishes has subsided, and the schools are dispersing, or migrating to nighttime feeding grounds. It is almost dark — only a trace of fading sunlight remains on the water's surface overhead. The large piscivores have withdrawn, and apparently the severe danger that prevailed moments earlier has passed (Hobson 1968, 1972).

Clearly twilight is a critical period for many fishes. It is so critical, in fact, that certain visual features of many species seem specially designed for better vision during this brief period even though it is only a small segment of the 24-hour day. Important studies by Munz and McFarland (1973) have shown that twilight is slightly bluer than the light of day or night. Significantly, they have also shown that some of the light-receiving elements in the eyes of many coral-reef fishes appear more sensitive to this unique quality of twilight (which is apart from the light's brightness) than to the quality of light at other times. This is a striking find, because the study included both diurnal and nocturnal fishes. Munz and McFarland hypothesized that this added sensitivity to the quality of twilight, which presumably lets them see slightly better at this time than they could otherwise, is an adaptation to the severe evolutionary pressures that have long been exerted on predator-prey interactions during this critical period. But sensitivity to twilight blue is a feature of predators as well as prey. We still must ask why predators become relatively more effective during twilight.

The visual equipment of piscivorous fishes may be better suited after all to the half-light of dusk than is the visual equipment of their prey. Fishes on tropical reefs, including prey of the piscivores, tend to be most active either by day, or by night (Hobson 1965, 1968, 1972, 1974, Starck and Davis 1966, Vivien 1973), and adaptations to these activities quite likely limit their abilities during the transition periods. The typical diurnal fishes, including various wrasses, butterflyfishes, and damselfishes, feed on small organisms, a task requiring exception-

ally sharp vision. On the other hand, most of the nocturnal fishes, including cardinalfishes, squirrelfishes, and soldierfishes, feed on comparatively large prey, but in relative darkness, a task requiring sensitivity to dim light (Hobson 1974). The two groups, then, have different visual needs; in fact, they accentuate aspects of vision that tend to be mutually exclusive; visual structures that stress perception of detail are poorly suited to dim light, whereas visual structures that stress sensitivity to dim light are poorly suited to perceiving detail (Walls 1942).

Recognizing these relationships, Munz and McFarland (1973) examined the eyes from a limited number of coral reef fishes and found that visual structures in the diurnal species differed from those in the nocturnal species precisely as might have been predicted based on their contrasting feeding circumstances. There were only two piscivores in their sample — the jack, *Carangoides ajax*, and the grouper, *Epinephelus merra* — but significantly these constituted a third group which have eyes with visual structures intermediate between those in the diurnal and nocturnal groups, and which Munz and McFarland assumed to be twilight feeders. Perhaps this development should have been expected. These piscivores take relatively large prey, so are free of the need to perceive great detail; and they do not feed at night, so they are free of the need for extreme visual sensitivity. Consequently, during the transitions between day and night these predators should have a marked visual edge over at least many of their prey. They can see well enough in light that is too dim for those diurnal prey that have sacrificed visual sensitivity for visual acuity, and they have better attention to detail than is possible for those nocturnal prey that have sacrificed visual acuity for visual sensitivity.

Apart from any sensory advantage that piscivores may have during twilight, however, they unquestionably gain an edge by choosing the time and place of the attack. The prey can only respond. During most of twilight the sky is light, but little of the light penetrates the water. As a result, predators positioned near the bottom find prey in the water above them readily visible against a light background, but prey in the midwaters find predators below them hidden in the gloom (Hobson 1966, 1968, Munz and McFarland 1973). Obviously, under

these circumstances small fishes find life in the midwaters especially risky, and their reason for vacating this region is obvious. Schools, however, must remain in this highly vulnerable position through twilight even though many of the features that protect them in bright light have lost effectiveness. The colorations of their members, for example, are no longer helpful in masking individuals. Predatory fishes typically attack from below at this time, and each schooler is silhouetted against the bright surface — a distinct target (Hobson 1966).

Summary

Most fishes that prey on other fishes use one of four predatory tactics each of which is strongly reflected in its body features. They either (1) run down their prey with an overpowering charge (examples: jacks and billfishes), (2) ambush their prey (examples: scorpionfishes and flatfishes), (3) habituate prey to their apparent nonaggressiveness (examples: basses, snappers), or (4) stalk their prey (examples: barracudas and pikes).

These tactics relate closely to the defenses of their prey. Some prey defenses are behavioral, such as schooling and staying within reach of shelter, whereas others involve some adaptive body feature; for example, the development of spines, or concealing colorations. Generally, these defenses are used in combination. Schooling fishes, for instance, often have color patterns and other body features that make individuals in the assemblage less conspicuous and therefore poorer targets for predators. And small reef fishes that characteristically swim a distance from shelter often have body features that permit them to swim faster and so speed their retreat to cover when threatened.

Predator-prey interactions are strongly influenced by the varying characteristics of underwater light at different times of the day-night cycle because most of the fishes involved orient mainly by vision. Prey defenses are most effective during midday, and the smaller fishes are relatively secure then. The most successful predators at this time are those at the scene when prey fishes make momentary errors. Those best able to succeed are among the ambushers, stalkers, and those that have habituated prey to their apparent nonaggressiveness.

Predators that characteristically run down their prey with a highly overt, straightforward charge find suitable targets rare during midday because prey are unlikely to make a defensive error in their obvious presence. Most large piscivores find light at night insufficient for hunting, thus greatly reducing their threat to small fishes then. Many prey defenses, including schooling and remaining within reach of shelter, are greatly relaxed at this time.

Piscivores are most active during the transition between day and night, with their attacks peaking during twilight. Their major prey are primarily diurnal or nocturnal species ill-equipped for the rapidly changing conditions that prevail during the transition periods. At these vulnerable times most of the smaller reef fishes abandon the exposed midwaters, but schooling species, which are unsuited to shelter in the reefs, cannot do so, and are attacked severely. The major twilight attackers are those large, aggressive predators that are most inhibited in their feeding during midday.

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ZOOPLANKTERS THAT EMERGE FROM
THE LAGOON FLOOR AT NIGHT AT
KURE AND MIDWAY ATOLLS, HAWAII

Many zooplankters in nearshore marine habitats are in the water column at night, but spend the daytime sheltered on or near the sea floor (Emery 1968; Glynn 1973; Porter 1974). The diel movements these organisms make between the water column and the sea floor are major features of nearshore ecosystems, and strongly influence many of the fishes in these habitats (Hobson 1968, 1973, 1974, 1975; Hobson and Chess 1976, 1978). Some of these zooplankters are holoplanktonic forms that swarm close to bottom structures by day and disperse above the reef at night. Included are various calanoid copepods (e.g., *Acartia* spp.), cyclopoid copepods (e.g., *Oithona* spp.), mysids (e.g., *Mysidium* spp.), and larval fishes (Emery 1968; Hobson and Chess 1978). Although such forms often occur in caves and other reef openings large enough to accommodate their free-swimming habit, they should be distinguished from the many meroplanktonic forms that by day live in or on the substrate (although this distinction between meroplankton and holoplankton is not always clear-cut).¹ At least some of these neritic holoplankters seem just loosely associated with specific substrata. For example, by day the calanoid *A. tonsa* swarmed close to coral reefs in the tropical Atlantic (Emery 1968) and to kelp forests in the warm temperate eastern Pacific (Hobson and Chess 1976), and also occurred in open waters offshore (Fleminger 1964). The meroplanktonic forms which by day characteristically assume what is essentially a benthonic mode have a much stronger affinity to specific nearshore substrata, and these are the major topic of this paper. Included are various polychaetes, ostracods, copepods, mysids, cumaceans, tanaids, isopods, gammarid amphipods, and various larval forms (Hobson and Chess 1976, 1978, in prep.).

Two recent studies, one on the Barrier Reef (Alldredge and King 1977) and the other in the

Philippine Islands (Porter et al 1977; Porter and Porter 1977), have attempted to quantify the emergence of zooplankters from various coral-reef substrata. These are important papers because they draw attention to what unquestionably is a highly significant and long-neglected aspect of nearshore ecosystems. We suspect, however, that there are problems with these studies. If so, the problems should be promptly recognized because undoubtedly they will spawn similar investigations by other workers elsewhere (e.g., see Randall et al. 1978). Alldredge and King collected their samples in Plexiglas² traps that rested on the bottom and retained organisms that rose into the water column; however, zooplankters from the surrounding water had access to these traps through gaps between the traps' rigid lower edges and irregularities on the sea floor. Earlier (Hobson and Chess 1978), we stated that these collections need to be repeated with this possibility of error eliminated. Obviously, if many zooplankters entered the traps from the surrounding water column, the samples cannot be considered measures of the organisms that emerged from the underlying substrata. The Porter group used traps that were tethered above the sea floor, and so would seem to have offered even greater access to zooplankters from the surrounding water. In fact, the probability that such forms entered the traps seems to us so great that we would have expected that their intent was simply to sample zooplankters near the reef. And yet, in prefacing their findings with statements like (p. 107) "... volumes of plankton produced per m² per hour by different reef substrates during the day and during the night are given in Table 1." they clearly implied that each trap sampled only those organisms that had risen from the substrate directly below it.

Our doubts about these studies, however, were moderated by limitations in our own knowledge of the phenomenon. We had worked extensively with these activity patterns as they relate to fishes (Hobson 1968, 1974; Hobson and Chess 1976, 1978) and had made inferences about the daytime modes of nocturnal zooplankters in nearshore habitats. Still, we had not satisfactorily distin-

¹We define meroplankton as those zooplankters that are in or on the substrate during part of the diel cycle, and holoplankton as those that are in the water column at all hours. As pointed out earlier (Hobson and Chess 1976), these terms have carried different meanings for different authors.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

guished the forms that by day assume essentially a benthonic existence on or in the bottom, from the forms that by day aggregate close to, yet free of, the substrate, or which migrate to deeper water. To increase our understanding of these activities and to acquire a firmer base upon which to assess other studies, we trapped zooplankters that emerged from various substrata in the lagoons of Kure and Midway Atolls, Hawaii during August 1977, making special effort to exclude forms from the surrounding water column.

Methods

Midway and Kure Atolls are about 90 km apart

at the northwestern end of the Hawaiian Archipelago. They are very similar, each having a lagoon that is relatively small (diameter about 8 km) and shallow (maximum depth about 15 m). All our study sites were in approximately 5 to 7 m of water near the outer leeward reefs.

We made seven paired collections, each pair at a different location. One of each pair sampled the organisms that rose from the substrate during the day, and the other sampled the organisms that rose from the same spot during the night. Of the substrates sampled, three were sand (two at Midway, one at Kure), two were a mixture of sand and coral rubble (one at Midway, one at Kure), and two were small heads of both living and dead coral

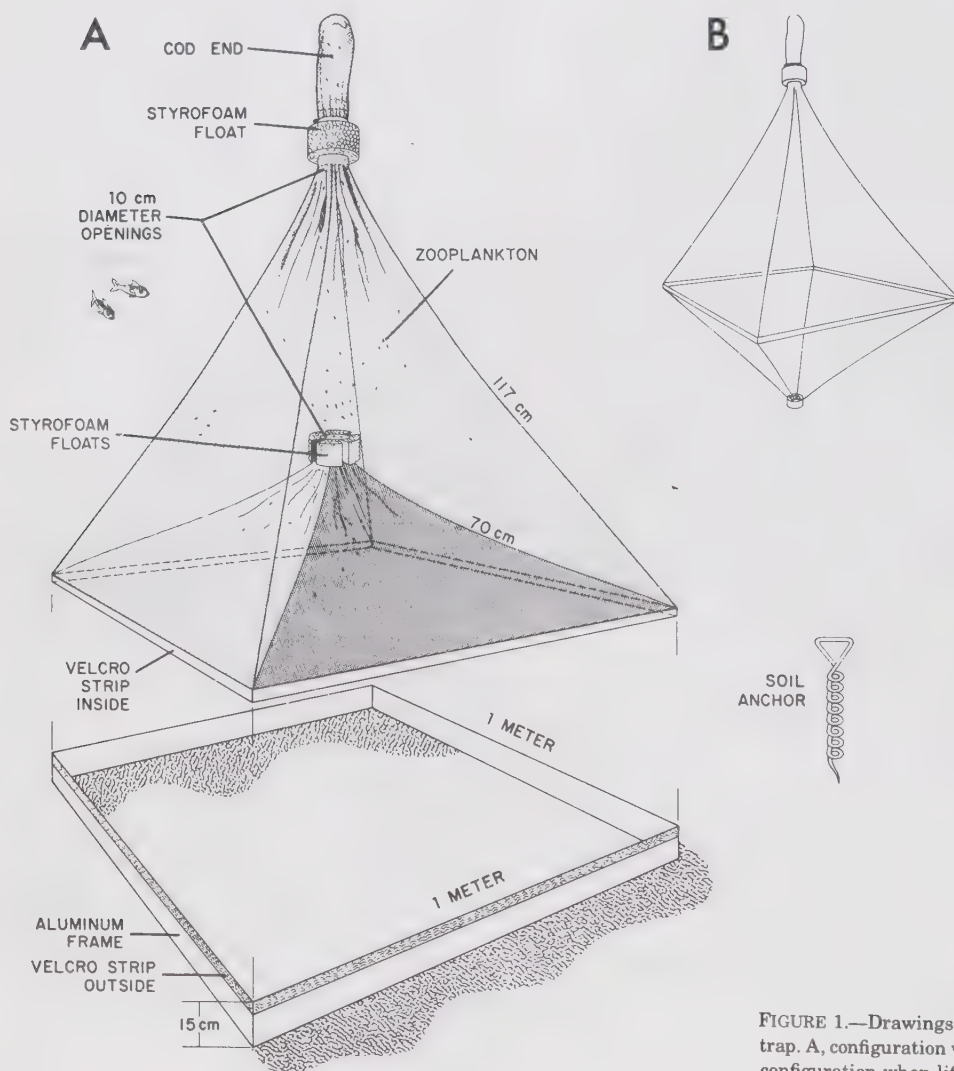


FIGURE 1.—Drawings of the meroplankton trap. A, configuration when set on bottom; B, configuration when lifted by diver.

(about 0.25 to 0.40 m²) surrounded by sand and coral rubble (one at Midway, one at Kure).

It was not our intent to characterize the meroplankton from each substrate—the collections were too few for this; rather, we sought only a general understanding of the types and numbers of organisms that emerge from the lagoon floor.

To begin each set of collections, we placed our trap (Figures 1, 2) in position between sunrise and 0800 h. First we buried the lower portion of the metal frame in the sand and secured it with soil anchors. A tight seal around the base of the trap was judged critical to prevent entry by organisms from the surrounding water. Next we attached the net (which had a 0.333-mm mesh) to this base and allowed it to remain in position throughout the day. We retrieved the net between 1730 h and sunset, washed all materials into the cod end, then removed the materials, and placed them in 10% Formalin. The net, with an empty cod end in place, was then reattached to the frame and left in place



FIGURE 2.—The meroplankton trap in place to sample organisms that emerge from sand in the lagoon of Midway Atoll. If the trap had not been designed to exclude holoplankters, we believe the collections would have included, among other holoplankters, calanoid copepods (*Acartia* sp.) that swarmed close to the adjacent reefs by day, including at their bases, and dispersed throughout the area at night.

throughout the night. The following morning, again between sunrise and 0800, the entire trap—base as well as net—was retrieved, and the collected organisms placed in preservative as before. Having thus completed one set of collections, we moved to another site and repeated the procedure. (We would have reversed the order of collections in some sets, e.g., nighttime first, if appreciable numbers of organisms had been taken by day; as it turned out, however, essentially all organisms were taken in the nighttime samples, as detailed in the Results.)

Our trap worked as follows: Organisms rising from the substrate inside the trap swam upward through the small upper opening of the inner cone and entered the space within the larger outer cone (Figure 1A). Some may have continued up into the cod end, which floated above, but this had no bearing on the collections. When the organisms returned toward the sea floor all except those that happened to descend through the small orifice of the inner cone were trapped where the two cones converged at their common base. In retrieving the net, we reached in under the edge attached to the metal frame and grasped the inner cone around its smaller orifice, thus closing it. We then pulled this out, thus everting the inner cone and producing a diamond-shaped bag (Figure 1B) with the orifice closed in our grasp at one end and the cod end at the other. We then towed the net back to the boat, still enclosing the smaller orifice in our grasp, so that, as we swam, all materials inside were swept back into the trailing cod end.

Results

The organisms collected by our trap, day and night, are listed in Table 1. The general absence of organisms in the daytime collections was predictable, based on the many reports which have concluded that the diel emergence of such forms is primarily a nocturnal phenomenon (see references listed above). Among organisms we observed swarming close to reef structures in the vicinity of our trap during the day were calanoid copepods (most of them *Acartia* sp.), mysids, and larval fishes. Although such forms disperse in the water column at night (Emery 1968; Hobson and Chess 1976, 1978), their absence from our trap collections is consistent with the contention that the holoplanktonic forms associated in varying degree with the reef are distinct from those organisms that live by day in or on the substrate.

TABLE 1.—Organisms trapped by day and night at Kure and Midway Atolls.

Zooplankton category	Day (n = 7)		Night (n = 7)	
	Percent occurrence	Mean no. individuals	Percent occurrence	Mean no. individuals
Foraminiferans ¹	43	2.9	100	18.9
Polychaetes ²	29	0.5	100	7.3
Gastropods ³	57	0.1	100	7.0
Ostracods ⁴	0	0.0	86	1.7
Calanoid copepods ⁵	0	0.0	100	17.7
Cyclopoid copepods	0	0.0	43	1.4
Harpacticoid copepods ⁶	0	0.0	100	31.0
Mysids	0	0.0	14	0.1
Cumaceans	0	0.0	29	0.6
Tanaids ⁷	0	0.0	86	11.9
Isopods ⁸	0	0.0	71	3.0
Cirripedian larvae	0	0.0	29	0.6
Gammarid amphipods ⁹	0	0.0	100	40.1
Caprellid amphipods	0	0.0	43	1.0
Caridean larvae	0	0.0	43	60.9
Caridean adults and juveniles	0	0.0	86	18.4
Reptantian zoea	0	0.0	57	17.0
Brachyuran megalops	0	0.0	71	6.3
Anomuran glaucothoë	0	0.0	43	1.3
Chaetognaths ¹⁰	0	0.0	57	5.9
Ascidian larvae	0	0.0	14	1.0

¹All foraminiferans were either *Tretomphalus* sp. (72%) or *Amphistigina* sp. (28%).

²The major polychaete was *Polyophthalmus* sp.

³Included one 8-mm dorid opisthobranch; the rest were prosobranchs <3 mm long.

⁴The major ostracod was a species of *Cylindroleberdinæ*.

⁵All identifiable calanoids were *Paramisophria* sp., probably undescribed (Abraham Fleminger, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. April 1978).

⁶All identified harpacticoids were of a species of the family Peltidiidae.

⁷All the tanaids appeared to be of a species of *Leptochelia*, close to *L. dubia* (see Hobson and Chess 1976).

⁸Major isopods were: *Cirolana* sp., *Ianiropsis* sp., *Munna* sp., anthurids, and cryptoniscid larvae.

⁹Gammarids included: *Aoroides* sp., *Dexaminoides orientalis*, *Liljeborgia* sp., a eusirid, an oedicerotid, and a phoxocephalid.

¹⁰All chaetognaths were *Spadella gaetanoi* (A. Alvarino, Fishery Biologist, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038, pers. commun. Sept. 1978).

Discussion

Our collections and collecting sites were too few to comprehensively quantify the zooplankters that emerge from the lagoon substrata at Kure and Midway Atolls. Despite its limitations, however, this study increases our understanding of the kinds of organisms that have this habit. Furthermore, it indicates there may be serious problems with the more extensive studies of Alldredge and King (1977), Porter et al. (1977), and Porter and Porter (1977).

Certainly some of the differences between their samples and ours are unrelated to sampling problems. We assume, e.g., that the zooplankton fauna at Kure and Midway Atolls is distinguishable from the zooplankton fauna in the more tropical latitudes of the western Pacific Ocean where the Alldredge and Porter groups studied. It is unlikely, however, that zoogeographic variations can account for certain of the more striking differences

between their samples and ours. The predominant forms in their collections were calanoid and cyclopoid copepods. Alldredge and King (1977) calculated that during the night a mean of 6,679 calanoids emerged from each square meter of the reef face, and Porter et al. (1977) reported that over 10,000 calanoids emerged during the night from each square meter of branching coral in their study area. In comparison, our night-long collections from a variety of substrata, including coral, yielded a mean of only 17.7 calanoids/m². Of course, we did not sample a well-developed reef. Only two of our sites included living coral, and these were isolated heads (our traps required a bed of sand). So habitat features could have contributed differences between the collections. Nevertheless, if one considers the species of calanoids and cyclopoids collected by Alldredge and King, there are strong indications that the large numbers reported were inflated by holoplanktonic forms. The only calanoids and cyclopoids they identified were *Acartia* spp. and *Oncaea* spp. Species of these two genera are exceedingly numerous in the water column during both day and night (see Emery 1968; Hobson and Chess 1976), and we question whether they could in fact assume a benthonic mode. As stated (Hobson and Chess 1978:149) "We would expect organisms that live in the substrate by day to have morphological features reflecting this habit that distinguish them from holoplanktonic relatives at the generic level or higher." Although the Porter group did not identify their calanoids and cyclopoids to lower taxa, they too sampled western Pacific reefs and so the copepods that similarly dominated their collections may well have been the same, or very similar, to those taken by Alldredge and King. All our calanoids, on the other hand, appeared to be referable to the little known genus *Paramisophria* (Abraham Fleminger, Associate Research Biologist, Scripps Institution of Oceanography, La Jolla, CA 92038, pers. commun. April 1978). This fact agrees with our contention that zooplankters which periodically enter the substrate should be morphologically distinctive. If the diurnal benthic mode of this species is a generic characteristic, which seems probable, then its poorly known status likely stems from failure to be sampled by standard plankton-collecting techniques.

During a marine survey of the Palau Islands, Randall et al. (1978) attempted to measure the zooplankters that emerged from the sea floor using traps "... built according to the design of Porter

and Porter (1977).” Their samples, taken above coral and sand substrata, included far fewer copepods than the Alldredge and Porter collections (but many more than ours); nevertheless, they recognized the presence of holoplanktonic forms (e.g., siphonophores, crustacean and fish eggs, and fish larvae), which they assumed “. . . either swam (or were carried) under the base of the trap from the open water . . .”

So we believe that the studies by the Alldredge and Porter groups are flawed by the unrecognized occurrence in their samples of organisms from the surrounding water column. At Enewetak Atoll (Hobson and Chess 1978), we concluded that many of the zooplankters above lagoon reefs at night are visitors from the deeper water. If this circumstance existed where Alldredge and Porter set their traps, then their collections probably included deep-water forms. If so, the figures presented as measures of zooplankters that emerge from defined areas of particular nearshore substrata probably include not only holoplankters associated by day with other nearshore substrata but also holoplankters from outside the nearshore realm.

We consider our collections conservative estimates of the numbers of organisms that emerge from the sampled substrata. It may be that some forms which ordinarily rise into the water column were inhibited by our trap, and undoubtedly some that rose into the trap found their way back to the sea floor. But we feel our trap should have been as effective in capturing emerging zooplankters as those used by the Alldredge and Porter groups. Possibly some strictly benthic forms entered our samples by climbing up the inside of the trap. The few prosobranch gastropods that were taken may have been trapped this way, although they were small enough to have been swept up into the water column by surge, or perhaps to possess some flotation device that periodically permits a planktonic mode, as is the case with certain foraminiferans (e.g., *Tretomphalus* and perhaps *Amphistigina*). Significantly, most of the organisms collected belong to groups that include forms we have collected in the water column at night elsewhere: e.g., the foraminiferan genus *Tretomphalus* (at Majuro and Enewetak Atolls: Hobson and Chess 1973, 1976); the polychaete genus *Polyopthalmus* (at Enewetak Atoll: Hobson and Chess 1978); and the ostracod subfamily *Cylindroleberdinae*, the tanaid genus *Leptochelia*, the isopod genera *Cirolana* and *Munna*, and family Anthuridae, the

gammarid genus *Aoroides*, and families Eusiridae, Oedicerotidae, and Phoxocephalidae (at Santa Catalina, southern California: Hobson and Chess 1976, in prep). The forms that predominated in our collections belong to groups that were only relatively minor elements in the Alldredge and Porter collections. Most, in fact, were lumped by Porter et al. (1977) in their summarizing Figure 2 as “miscellaneous.” This is not because they took fewer of these forms than we did, but rather because copepods and larvaceans so dominated their collections.

We believe that the major difference between our collections and those of the Alldredge and Porter groups is that we excluded organisms from the surrounding water column. Alldredge and King (1977) were aware that outside organisms could enter through the gaps around the base of their traps, but seemed more concerned about organisms inside that might have escaped. They dismissed both possibilities as significant sources of error with the statement (p. 318) “. . . as many plankters may also enter the trap through these gaps as escape through them.” But because these devices were, after all, traps, probably many more zooplankters came in than went out. And if in fact zooplankters entered the traps through these gaps, it seems certain that forms from the surrounding water, including holoplankters, were continuously captured. Porter et al. (1977) reported about 1.5 to 2 times as many zooplankters as did Alldredge and King. They attributed this difference to more effective methods and equipment, but their traps, tethered above the reef, may simply have been more readily entered by holoplankters. This would also account for the relatively large numbers of zooplankters they trapped by day. Both studies may have suffered from a misconception about the movements of these organisms. Alldredge and King doubted that many escaped through the gaps around the bases of their traps because they assumed (p. 318) “. . . emerging plankton swim primarily upward . . .” The Porter group would seem to have based their trap design—inverted cones tethered above the bottom—on the same assumption. But while these animals certainly rise progressively higher in the water column after emerging from the sea floor, generally they swim—some flit—in short, irregular tangents more horizontal than vertical (based on our direct observations of a wide variety of forms in many locations). In any event if holoplankton did enter these traps in significant numbers, then

the samples taken should not be presented as measurements of the forms that emerged from the underlying substrata.

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EFFECT OF ULTRAVIOLET IRRADIATION ON EGGS AND LARVAE OF THE NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND THE PACIFIC MACKEREL, *SCOMBER JAPONICUS*, DURING THE EMBRYONIC STAGE*

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Abstract—Anchovy and mackerel eggs and yolk-sac larvae were exposed to UV radiation in the bioactive band of wavelengths between 280 and 320 nm, the UV-B region of the spectrum. Irradiation levels were based upon predicted UV-B increases that would result from anthropogenic diminution of Earth's protective ozone shell. Dose-response relationships for mortality and histological and morphological effects were determined for two different spectral energy compositions, using FS-40 sunlamps and two filter combinations. Anchovy were more sensitive than mackerel to UV-B. Data for anchovy were analyzed in terms of DNA-effective doses, i.e. the integrated spectral fluence (in $J/m^2/nm$) with the energy at each nm weighted by its effectiveness relative to the Setlow generalized DNA action spectrum. Fifty per cent of anchovy survived a cumulative DNA effective dose of $1150 J \cdot m^{-2}$ over a 4-day period. In the surviving larvae, irradiation induced lesions in the brain and eye, caused marked dispersion of pigment within melanophores and retarded growth and development. At the lowest dosage used, $760 (J \cdot m^{-2})_{DNA \text{ eff.}}$, growth was retarded and brain lesions occurred in anchovy. Calculations of Smith and Baker (in this issue) indicate that in clear ocean water a significant incidence of lesions and retardation of growth in anchovy could occur at the surface at a 25% reduction in ozone and down to 3.5 m at a 50% reduction. Eggs and larvae of anchovy occur at these depths.

INTRODUCTION

Evidence exists for lethal or detrimental effects of UV irradiation on eggs and larvae of fishes. This literature, reviewed by Eisler (1961), describes effects in fresh water fishes, particularly the salmonids, and little information exists on pelagic marine fishes. More recently Marinaro and Bernard (1966) and Pommeranz (1974) showed that pelagic eggs of marine fishes may be quite sensitive to natural UV irradiation. Radiometric measurements in past studies, however, are inadequate for predicting the effects on marine fishes of increased solar UV radiation resulting from diminution of the ozone layer. The objective of this study was to describe the effects of UV-B radiation on eggs and larvae of two pelagic marine fish, the northern anchovy (*Engraulis mordax*) and the Pacific mackerel (*Scomber japonicus*), and to estimate the potential hazard to these species of increased levels of solar UV irradiation.

Both species occur in the egg and larval stages in the upper 1 m of the water column (Ahlstrom, 1959; Ahlstrom and Stevens, 1976), and are, therefore, exposed to significant levels of UV radiation in the

sea. These species are more vulnerable to the direct effect of UV irradiation during the egg and larval stage than at any other time because of their near-surface distribution, inactivity, lack of scales or other integument, and the fact that the sensitive processes of organogenesis are taking place.

In this study we examined the effects of UV irradiation during the embryonic period, that is, during the first 4–5 days of life when the fish exist as eggs and small larvae (3–4 mm) subsisting on yolk. At the close of this period, the eyes become pigmented and functional, the jaw becomes functional, nearly all the yolk is exhausted, and feeding begins.

MATERIALS AND METHODS

Apparatus. A temperature-controlled white fiberglass water table, 366 cm long, 122 cm wide and 15 cm deep, was installed on the roof and two were installed in the marine aquarium of the Southwest Fisheries Center at La Jolla, CA. Each table was ruled into 144, 15 cm squares and each square assigned a unique number to identify it for radiometric calibrations and assignment of test containers. An aluminum framework enclosing the rooftop water table (the solarium) provided support for fluorescent UV lamps 122 cm above the water surface (Fig. 1). The frame was enclosed with "Screen Glass®" and air temperature within the enclosure was regulated with an air-conditioner and heater. The Screen Glass transmitted about 20%,

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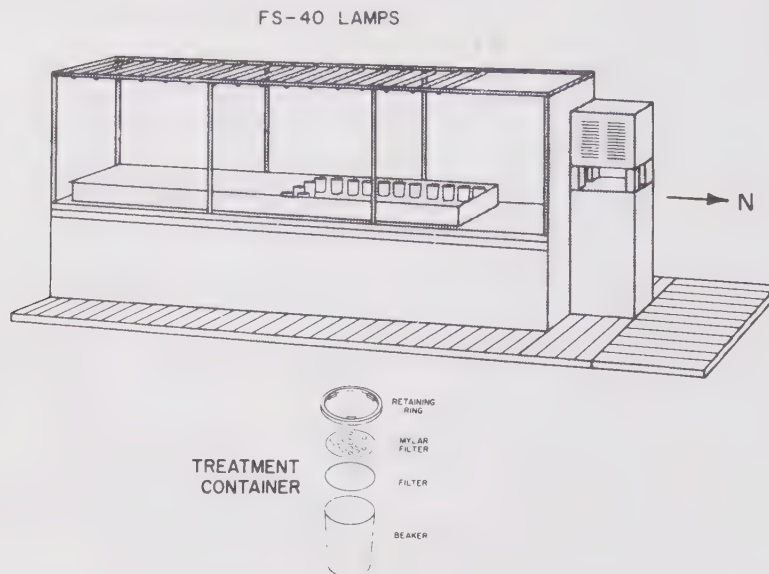


Figure 1. Diagram of roof top facility (solarium) indicating placement of treatment containers, artificial UV-B sources, and north-south orientation of treatment table. Inset shows exploded view of individual treatment container and associated filters.

of the solar UV-B but transmitted 92–94% of the natural radiation between 360 and 700 nm.

The banks of fluorescent lamps used in the aquarium experiments were mounted on large reinforced plywood sheets laminated with mirror-polished aluminum (Alzak®) to provide optimum reflective efficiency for both visible and UV wavelengths. In the solarium, however, the UV-supplementing FS40 lamps were not provided with reflectors, in order to minimize shadows on the treatment table.

In the aquarium apparatus, visible light was provided by "Chroma 50®" fluorescent lamps, which give a fair approximation to the shape of the visible solar spectrum, and the UV energy by FS-40 fluorescent sunlamps. The tubes were mounted on 5.46 cm centers; every third lamp a UV source. The aquarium luminaires were adjusted to either 93 cm or 61 cm above the water surface in the treatment containers. Before use, all lamps were aged for approx. 200 h in order to reach a relatively flat portion of the energy decay curve supplied by the manufacturer.

Irradiance of the treatment tables varied from point to point. Although these differences were not large, they were carefully measured, and taken advantage of by appropriate placement of treatment containers on the tables. Examples of the non-uniform flux distributions from artificial sources are given in Fig. 2 which shows computer-generated plots of the effect for the solarium and one of the aquarium tables. Additional smoothing of the contours was achieved by covering the ceiling and walls of the aquarium room with heavy aluminum foil.

The duration and intensity of artificial irradiation was controlled by switching the fluorescent lamps. In the aquarium studies, the Chroma 50 and FS-40 lamps were switched in accordance with Fig. 3. The rationale for this pattern of onset and offset steps takes crude account of the natural rise and fall of radiant energy on a typical day, as well as the desire to minimize any trauma to the animals. Figure 3 also indicates the approximate course of daily treatment when natural and artificial sources were combined in the solarium. All irradiation schemes were centered on local apparent noon.

Radiometry, sources, and filters. Various integrating instruments (sunburn meter—Solar Light Company; UV-B radiometer—Optronic Laboratories; deck cell illuminometer) were used for photometric and radiometric determinations during the first months of research because of the lack of a UV-sensitive spectroradiometer. It was later

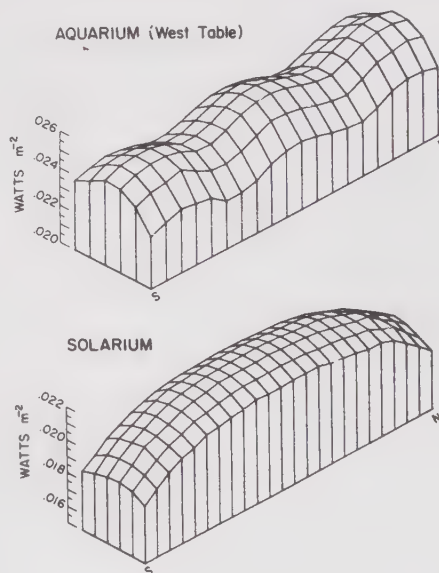


Figure 2. Computer-generated plots showing non-uniformity of irradiance over treatment tables when all UV lamps are lit. For artificial UV-B sources, lamp height was 93 cm in aquarium table and 122 cm in solarium. The aquarium table plot shows the effect of lamp end cooling.

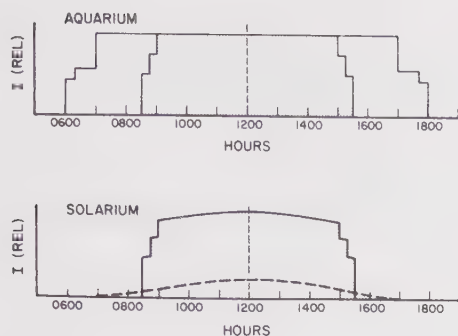


Figure 3. Schematic representation of the irradiation regimen for aquarium and for solarium. Shaded areas show UV-B component alone. In the solarium, area under curve results from switching on UV-B lamps to supplement natural component (area under dashed curve). [Local apparent time.]

possible to reconstruct the test situation and to recalibrate our measurements using a recording spectroradiometer (Optronic Model 741-V). This instrument scanned automatically from 250 to 800 nm with a 1 nm readout from 250 to 360 nm and 2 nm readout at longer wavelengths. Wavelength accuracy using a low-pressure Hg lamp for calibration was ± 0.5 nm and the spectroradiometric accuracy was $\pm 3\%$. The dynamic range was seven decades in intensity owing to the use of a logarithmic amplifier. Intensity calibration was done by use of a 1,000 W tungsten-halogen standard lamp operated at $8,000 (\pm 0.1\%)$ A on a 2-m photometric bench and is traceable to the National Bureau of Standards. Doses were determined by measuring the absolute irradiances (in $\text{W}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$) integrated from 285 to 300 nm, multiplied by the duration of the experiment in h, and expressed in $\text{J}\cdot\text{m}^{-2}$.

The eggs and larval fish were irradiated in two ways: either with daylight supplemented by artificial UV-B radiation (solarium system), or by a combination of UV-B and visible light from artificial sources (aquarium system). Natural radiation was monitored, both inside and outside the canopy of the solarium, and its spectral energy distribution determined for different days.

One- ℓ polypropylene beakers, coated with black tape on the outside and containing 800 ml of filtered seawater were used as test containers. Each beaker was provided with a cap which held the treatment control filter (or filters) appropriate to a given condition (Fig. 1).

Various plastic materials were used in the cap for control of dosages and to prevent evaporation in the containers. They were: Polystyrene—clear sheet, 0.13 mm thick, Cellulose triacetate—clear sheet, 0.13 mm, Aclar®—clear sheet, 0.13 mm, Polystyrene 666-U—molded discs, 0.97 mm, Mylar—clear sheet, 0.13 mm.

Both polystyrenes and cellulose triacetate were used to provide different shortwave cutoff characteristics in the UV-B spectral region. The Aclar®, which transmits well in the UV-B region, was used to control evaporation, with negligible attenuation of UV-B. Mylar, which transmits little UV-B, was used in solid sheets to cover the control containers (Fig. 4). The integrated transmittance of Mylar in the UV-B band, 285–320 nm, is about 4% of that for CTA and when weighted by the Setlow DNA action spectrum (Green and Miller, 1975), the effective transmittance of Mylar is 0.6% of that for CTA.

The experimental dosage levels (other than zero or 100% of full available intensity) were controlled by use of circular

Mylar filters that were perforated by holes of various sizes, as seen in Fig. 1. Transmission of these filters was determined by the hole size with the number of holes and center-to-center distances held constant. When used with an Aclar® filter at one end of the range and a solid Mylar at the other, the range of percentages of incident UV-B flux was: 94.0, 69.6, 49.7, 29.0, 23.5, 18.9, 10.7, ~ 0 .

The optical geometry resulting from use of perforated filters produces non-uniformity of irradiation across the water surface. The effect is greatest for the direct solar component of natural UV-B under lower-transmittance filters, but considerably less for extended sources (sky dome and fluorescent luminaires) and larger hole sizes.

Experimental design. Eggs of anchovy and mackerel were obtained from brood stock maintained in reproductive condition throughout the year at the Southwest Fisheries Center (Leong, 1971, 1977). In most experiments, eggs were held for 24 h at 16°C before stocking to reduce incidence of non-viable eggs. Each treatment and control consisted of 15 test containers stocked with 50 eggs each. Areas of similar incident UV-B irradiation on each water table were identified by square number and treatment and control containers were assigned a square within these fields on a random basis. Specific fields were selected for specific treatments to increase uniformity of dosage within a treatment; controls were partitioned equally in different fields but square assignment within a field was random. Areas of high variability such as along the sides and ends of tables or beneath the ends of lamps in the west aquarium table were avoided.

Experiments ended at the close of the embryonic period. Anchovy were exposed for about 6–10 h in the egg stage and 15–20 h as yolk-sac larvae, and mackerel about 6–16 h as eggs and 25–32 h as larvae. Three experimental conditions were used: in the first, we used the solarium enclosed by Screen Glass®, the source of UV energy was FS-40 lamps filtered by polystyrene caps on the beakers, and the sun was the source of visible energy (anchovy exps. 1 and

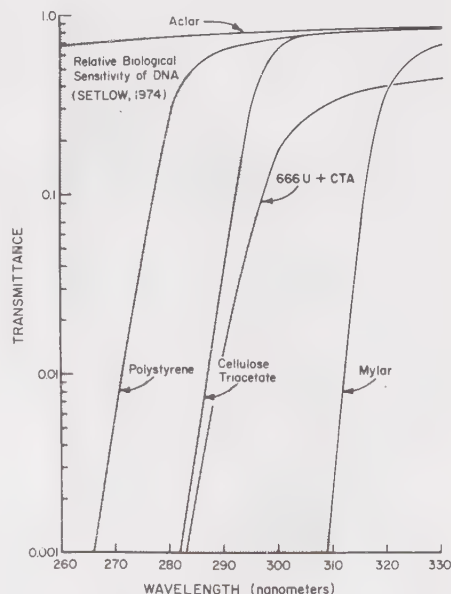


Figure 4. Spectral transmittance curves for the plastic filter materials used in the experiments. The shaded region represents the relative biological sensitivity of DNA as a function of wavelength.

Table 1. Effect of UV on anchovy during embryonic stage

Expt. no. (date)	UV source	Visible source	Filter ¹	egg h	UV lamp exposure h	larvae h	Total UV lamp exposure h	Total visible dosage meter-candle h	Dosage ² Jm ⁻²	Number of containers	Mean number of survivors ³ $\bar{x}$	Percent survival normalized to controls
1 (5-2)	FS40	Solar	M	0	0	0	0	12,000	0	15	21.67	100.0
			PS	10.00	15.00	15.00	25.00	12,000	13,000	15	19.47	89.8
			PS	10.00	15.00	15.00	25.00	12,000	26,900	15	11.67	53.9
			PS	10.00	15.00	15.00	25.00	12,000	41,100	13	8.77	40.5
2 (6-7)	FS40	Solar	M	0	0	0	0	12,000	69,600	15	0.33	1.5
			PS	10.00	17.00	17.00	27.00	9,240	0	16	30.75	100.0
			PS	10.00	17.00	17.00	27.00	9,240	14,200	15	30.26	98.4
			PS	10.00	17.00	17.00	27.00	9,240	29,400	15	19.20	93.2
3 (7-25)	FS40	Chroma 50	M	0	0	0	0	9,240	91,100	15	0.33	1.1
			CTA	6.20	21.00	21.00	27.20	4,400	0	15	25.40	100.0
			CTA	6.20	21.00	21.00	27.20	4,400	68,300	15	23.10	90.9
			CTA	6.20	21.00	21.00	27.20	4,400	94,000	14	9.57	37.7
4 (8-1)	FS40	Chroma 50	CTA	6.20	21.00	21.00	27.20	3,770	162,000	15	0.13	0.5
			M	0	0	0	0	3,930	0	15	41.20	100.0
			CTA	5.25	21.00	21.00	26.25	3,930	62,500	15	39.07	94.8
			CTA	5.25	21.00	21.00	26.25	3,930	90,400	15	30.60	74.3
5 (8-22)	FS40	Chroma 50	CTA	5.25	21.00	21.00	26.25	3,360	115,000	15	16.47	40.0
			CTA	5.25	21.00	21.00	26.25	3,360	148,000	15	0.33	0.8
			M	0	0	0	0	4,360	0	15	22.93	100.0
			CTA	6.58	19.75	19.75	26.33	4,360	92,000	15	6.53	28.5
6 (12-19)	FS40	Chroma 50	CTA	6.58	19.75	19.75	26.33	4,360	109,000	15	1.47	6.4
			CTA	6.58	19.75	19.75	26.33	4,360	117,000	15	1.13	4.9
			M	0	0	0	0	4,300	0	15	40.50	100.0
			666-U + CTA	6.00	20.33	20.33	26.33	4,300	248,000	16	19.3	47.6

¹M = Mylar; PS = Polystyrene; CTA = Cellulose triacetate; 666-U = Polystyrene 666-U.²275-320 nm PS experiment; 285-320 nm CTA experiment.³ $\bar{x}$ = Mean number survivors per container; s = Standard deviation.

Table 2. Effect of UV on mackerel during embryonic stage

Expt. no. (date)	UV source	Visible source	Filter ¹	egg h	UV exposure larvae h	Total UV lamp exposure h	Total visible dosage meter-candle h	Dosage ² Jm ⁻²	Number of containers	Mean number of survivors ³ $\bar{x}$	s	Percent survival normalized to controls
1 (4-25)	FS40	Solar	M	0	0	0	11,400	0	15	43.93	2.60	100.0
			PS	10.00	15.58	25.58	11,400	25,400	15	40.93	4.13	93.2
			PS	10.00	15.58	25.58	11,400	38,400	15	43.27	4.48	98.4
			PS	10.00	15.58	25.58	11,400	65,500	15	23.07	9.85	52.5
2 (7-19)	FS40	Chroma 50	M	0	0	0	5,780	0	15	37.26	11.16	100.0
			CTA	16.00	17.50	32.50	5,780	127,000	15	20.07	9.11	53.8
			CTA	16.00	17.50	32.50	5,780	159,000	15	7.13	8.43	19.1
			CTA	16.00	17.50	32.50	4,940	199,000	15	0.27	0.59	0.7
3 (8-9)	FS40	Chroma 50	M	0	0	0	4,730	0	15	39.00	7.14	100.0
			CTA	7.75	17.25	25.00	4,730	65,600	15	38.53	7.38	98.8
			CTA	7.75	17.25	25.00	4,040	91,300	15	43.13	2.69	110.6
			CTA	7.75	17.25	25.00	4,730	94,900	15	43.73	4.04	112.1
4 (8-30)	FS40	Chroma 50	M	0	0	0	4,730	120,000	15	31.67	13.96	81.2
			CTA	6.00	21.00	27.00	4,400	0	15	46.20	2.76	100.0
			CTA	6.00	21.00	27.00	4,400	93,300	15	33.73	9.16	67.5
			CTA	6.00	21.00	27.00	4,400	125,000	14	19.00	14.33	41.1
			CTA	6.00	21.00	27.00	4,400	177,000	15	8.07	8.22	17.5

¹M = Mylar; PS = Polystyrene; CTA = Cellulose triacetate.²275-320 nm PS experiments; 285-320 nm CTA experiments.³ $\bar{x}$ = Mean number survivors per container; s = Standard deviation.

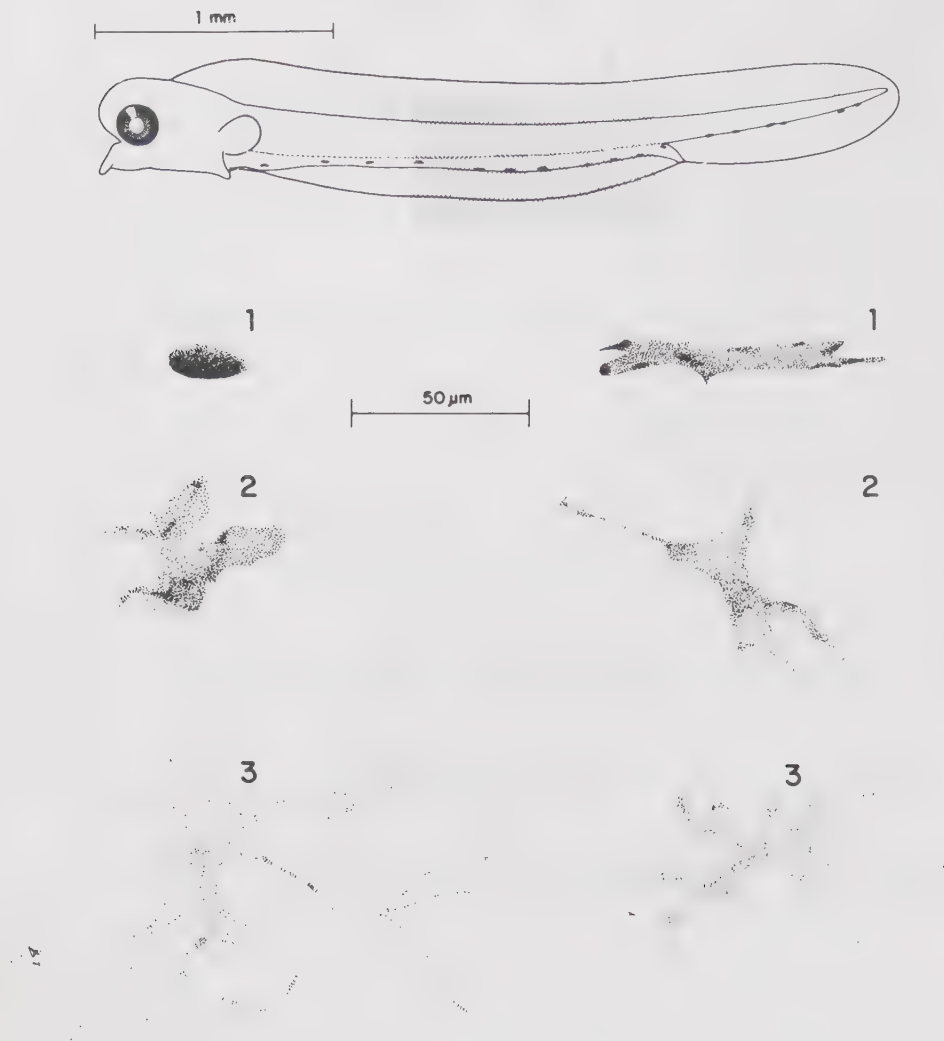


Figure 5. State of melanosome dispersion in Mylar control and UV-B irradiated larvae drawn to scale from photomicrographs. Shaded areas on larvae indicate areas on body used in anchovy for grading. Numbers are grades used to quantify dispersion: grade 1 was typical of controls; grades 2-3 occurred in irradiated specimens. Right and left columns of figure indicate the range of dispersion states included within a grade.

2, Table 1; mackerel exp. 1, Table 2); in the second, aquarium tables were used, the source of UV energy was FS-40 lamps filtered by cellulose triacetate (CTA) and the source of visible energy was Chroma 50® lamps (anchovy exps. 3, 4, and 5; mackerel exps. 2, 3, and 4); the third, the aquarium table was used with FS-40 lamps filtered by polystyrene 666-U and CTA (anchovy exp. 6).

Water temperature in the containers, and UV-B and visible flux were monitored continuously, and salinity, oxygen and ammonia at the beginning and end of each experiment. Salinity varied from 33.0 to 34.0‰, oxygen from 97.3 to 71.2% saturation, ammonia from 0.010 to 0.091 ppm and temperature from 16.3 to 17.0° C. Surviving

larvae were counted at the end of an experiment; some fixed in Bouin's solution for histological analysis, and the rest preserved in 3% formalin.

Formalin-preserved specimens from experiments employing CTA filters, were examined to determine effects of UV-B on morphology and pigmentation. We measured the standard length, body depth at the origin of the pectoral fin, maximum depth of the yolk-sac, eye pigmentation, and extent of pigment dispersion in melanophores of 32-85 larvae per treatment. Typically, five larvae per container within a treatment were measured, but numbers varied with the number of survivors. Larvae were assigned a grade of 1 to 3 on the basis of eye pigmentation: Grade

1, only a trace of pigment or pigment distributed around only the outer margin of the eye; grade 2, intermediate pigmentation; and grade 3, eye completely pigmented. The state of dispersion of the melanosomes (pigment granules) within the melanophores was estimated by assigning grade 1 to the completely aggregated condition and grade 3 to the fully dispersed (Fig. 5). In anchovy, two regions along the ventral margin of the body were graded, and in mackerel, because they had more melanophores, four regions were used: the dorsal surface of the head; yolk-sac; hind gut; and ventral margin of the body.

Complete sagittal serial sections cut at 5–6 μm were prepared from each specimen preserved for histological work. Slides from selected experiments were examined for the number of lesions in the brain and nuclear layer of the retina. Larvae were examined without knowledge of dosage to avoid interpretative prejudice. Lesions were defined as consisting of one or more spherical pycnotic nuclei surrounded by an extracellular vacuolated region, frequently containing eosinophilic cytoplasmic debris. To provide an index of damage as a function of dosage, we counted the number of lesions in the brain and eye in every section of a larva and divided the total by the number of sections examined. Incidence was defined as the average number of lesions in a tissue per section. The number of sections examined per larva varied, ranges for anchovy were: eyes, 33–40; brain, 27–43; and for mackerel: eyes, 45–55; brain, 41–50. Typically 12–15 larvae per treatment were examined but fewer in treatments with very low survival.

Survival in the controls varied among anchovy experiments from 43 to 80% and from 74 to 92% in mackerel, because of differences in egg viability between spawns (Tables 1 and 2). To adjust for these differences, we divided the percent survival in the treatments by that of the controls in each experiment. These normalized survival data were used to calculate a dose-response line using probit analysis (Finney, 1952). Adjusting the treatment data in this manner increases the survival probabilities, and thereby decreases the variance. This underestimate was proportional to the reciprocal of the percent survival of the controls and we have corrected the standard deviation by multiplying by this factor.

RESULTS

Survival

In experiments conducted in the aquarium using FS-40 lamps and cellulose triacetate filters (CTA), 50% of the anchovy survived a cumulative UV-B (285 to 320 nm) dosage of $91,200 \text{ J}\cdot\text{m}^{-2}$ (95% C.I. = $80,700\text{--}100,000 \text{ J}\cdot\text{m}^{-2}$) over a 4-day period (Fig. 6) and 50% of the mackerel survived a cumulative UV-B dosage of $125,000 \text{ J}\cdot\text{m}^{-2}$ (95% C.I. = $98,900\text{--}148,000 \text{ J}\cdot\text{m}^{-2}$) over a 4- to 5-day period (Fig. 7). When the energy from FS-40 lamps was filtered by polystyrene (PS), the LD_{50} occurred at lower dosages. In these experiments 50% of the anchovy survived a cumulative dosage (275–320 nm) of $31,000 \text{ J}\cdot\text{m}^{-2}$ (95% C.I. = $25,300\text{--}38,200 \text{ J}\cdot\text{m}^{-2}$) (Fig. 6), and data from a single experiment suggest that 50% of mackerel are able to survive a dose of about $65,500 \text{ J}\cdot\text{m}^{-2}$ over a 4-day period (Table 2, exp. 1). Differences in the dose-response relation between experiments employing CTA filters and those using PS filters may be attributed to differences in the spectral transmission of the two filters. The PS filter transmits about 30% of the energy at 280 nm whereas the CTA filter transmits less than 1% (Fig. 4). Thus, larvae and eggs under the PS filter received more energy in the shorter and more actinic wavelengths of the UV band. Under both experimental conditions, anchovy were more sensitive to UV irradiation than mackerel. The difference in the LD_{50} was about $34,500 \text{ J}\cdot\text{m}^{-2}$ under the two experimental conditions.

The likelihood of biological effects may be seriously underestimated if measurement of dose is based on integrated flux alone. Ozone diminution results in a disproportionately large increase in radiant energy in

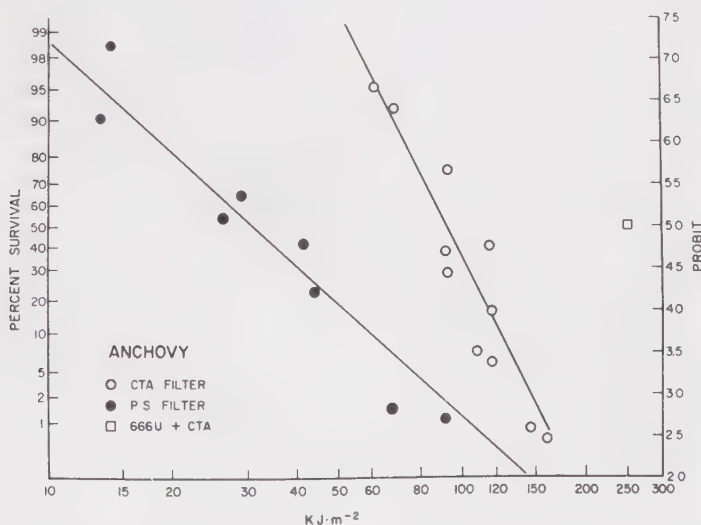


Figure 6. Per cent survival of northern anchovy at the end of the embryonic period (probit scale) and total cumulative dose of UV-B (log scale) in $\text{kJ}\cdot\text{m}^{-2}$, for three spectral energy distributions. Energy sources were: FS-40 lamps with cellulose triacetate filters (CTA); polystyrene filters (PS); and polystyrene 666-U + CTA. Lines are regressions of mortality probit on log dose and points are the mean survival for 15 containers.

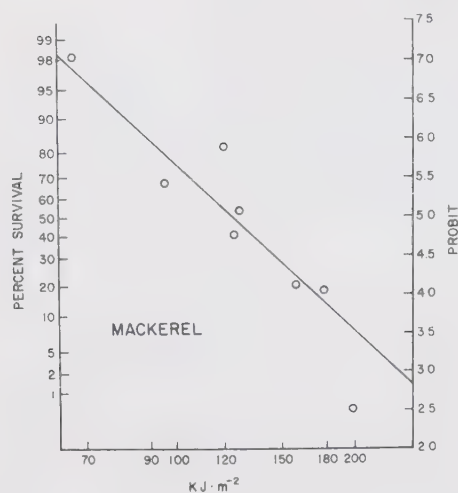


Figure 7. Percent survival of Pacific mackerel at the end of the embryonic period (probit scale) and total cumulative dose of UV-B (log scale) in $\text{kJ}\cdot\text{m}^{-2}$. Energy source was FS-40 lamps filtered by cellulose triacetate (CTA); points are mean survival for 15 containers.

that part of the UV-B spectral band to which larval fishes are the most sensitive. Thus, an effective dose must be based upon a weighting function that takes account of the wavelength dependency of biological action. Accordingly, we applied several existing weighting functions to the combined data from the CTA and PS experiments: germicidal action spectrum (Kaufman and Christiansen, 1972); Caldwell's generalized action spectrum (Green and Miller, 1975); and Setlow's action spectrum for DNA (Green and Miller, 1975). The spectral energy distribution for each treatment under CTA and PS was weighted by multiplying the energy at each nanometer by the appropriate coefficient from the particular weighting function and the weighted energy for a particular treatment integrated. Table 3 gives the unweighted energy per nanometer for the LD_{50} in the PS and CTA experiments upon which these calculations are based.

The weight that gave the best fit to regression of probit on log weighted dose for the combined data was the Setlow DNA action spectrum (Fig. 8). For example, the LD_{50} estimates for the CTA and PS experiments, when weighted by the Setlow DNA action spectrum, differed by only 8%, whereas they differed by 42% when weighted by the Caldwell action spectrum. As can be seen by comparing Figs. 6 and 8, the Setlow weighting function provided an adequate adjustment for the differences in spectral composition between the two experiments. The LD_{50} for anchovy using the DNA weighted dosages from the two experiments, was $1150 \text{ J}\cdot\text{m}^{-2}$ (95% C.I. = 990–1400).

As a test of this weighting procedure, we conducted an experiment using a filter combination (polystyrene 666-U + CTA) that produced a cutoff at a longer

wavelength than either PS or CTA filters (Fig. 4). In this experiment, $47.7 \pm 9.0\%$ of the anchovy larvae survived a dosage of $248,000 \text{ J}\cdot\text{m}^{-2}$. This dosage is much higher than those producing comparable survival in the other experiments (Fig. 6) but when weighted by the DNA action spectrum it is reasonably close to those values (Fig. 8). Thus, the Setlow DNA action spectrum was a relatively good model for predicting lethal UV-B effects in anchovy larvae under differing spectral energy distributions. This result not only unifies the results from experiments employing different spectral energy distributions but also makes possible calculation of dose levels that would occur under various conditions of ozone diminution.

Histological effects

Lesions occurred in the brain and the eye in anchovy and mackerel larvae surviving exposure to UV irradiation (Fig. 9). Incidence of lesions was higher in the PS experiments than in the CTA experiments as could be expected from the difference in spectral energy composition of UV-B. It required roughly twice the dosage to produce an equivalent response using CTA filters than when PS filters were used. For example, the mean incidence of eye lesions in anchovy was 0.53 ± 0.18 at a dosage of $45,000 \text{ J}\cdot\text{m}^{-2}$ in the PS experiments whereas it required a dosage of $94,000 \text{ J}\cdot\text{m}^{-2}$ to produce an incidence of 0.44 ± 0.28 in the CTA experiments. More specimens were examined histologically in the CTA experiments

Table 3. Dose per nm at the LD_{50} ¹ of northern anchovy larvae for polystyrene and cellulose triacetate filters under FS-40 lamps

Wavelength (nm)	Dose ($\text{J}\cdot\text{m}^{-2}$) PS	CTA	Wavelength (nm)	Dose ($\text{J}\cdot\text{m}^{-2}$) PS	CTA
276	8	—	299	839	2320
277	10	—	300	901	2640
278	14	—	301	939	2890
279	20	—	302	1010	3190
280	30	—	303	1070	3440
281	41	—	304	1070	3510
282	55	—	305	1130	3750
283	71	—	306	1160	3900
284	91	—	307	1190	3980
285	114	—	308	1200	4060
286	148	22	309	1240	4180
287	181	23	310	1280	4370
288	218	26	311	1370	4650
289	259	35	312	1440	4900
290	303	59	313	1460	5010
291	341	109	314	1360	4660
292	387	205	315	1270	4360
293	447	369	316	1200	4170
294	510	604	317	1170	4050
295	582	912	318	1130	3990
296	660	1270	319	1130	3930
297	716	1610	320	1100	3840
298	783	1990			

¹Sum of values in table are within 2% of integrated dosages given in text.

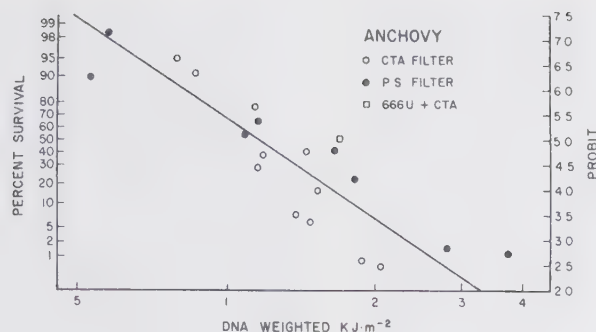


Figure 8. Per cent survival of northern anchovy at the end of the embryonic period (probit scale) and total cumulative dose of UV-B weighted by DNA action spectrum of Setlow (1974) using the analytical fit of Green and Miller (1975). Line is the regression of mortality probit on log dosage for the combined weighted data from the CTA and PS experiments.

and the incidence of lesions was plotted as a function of dosage (Fig. 10). Even at the lowest dosages employed in the CTA experiment, $63,000 \text{ J} \cdot \text{m}^{-2}$, incidence of lesions in the brain of anchovy was different from the control (t test, $P < 0.01$) and that in the eye was between the 5 and 10% probability levels. At $68,000 \text{ J} \cdot \text{m}^{-2}$, incidence of lesions in both brain and eye in anchovy were different from the control ($P < 0.01$ for brain; $P < 0.05$ for eye). Thus, significant damage to both brain and eye occurred after only 4 days at our lowest dosages.

The incidence of lesions in brain and eye was much higher in anchovy than in mackerel. At dosages near the LD_{50} for each species the incidence of eye lesions was about three times and brain lesions five times higher in anchovy than in mackerel. Eye lesions ranged from 5 to $48 \mu\text{m}$ (maximum dimension) in anchovy whereas in mackerel they were somewhat smaller, usually ranging from 5 to $10 \mu\text{m}$ and occasionally to $24 \mu\text{m}$. Lesions also occurred in the olfactory bulb in both species but were not evaluated. The treatments affected the rate of development of melanistic pigment in the eye. The proportion of larvae examined histologically with partially pigmented or unpigmented eyes increased in both species with dosage. This effect is described in more detail from morphological examination and is discussed in the next section.

Morphological effects

During the yolk-sac period, the yolk supply decreases as larvae increase in length and body depth; during the last day, the eye becomes progressively more pigmented, until at the end of the period eye pigmentation is complete and the yolk supply is nearly exhausted. At the end of our experiments, all larvae in the controls were at this later stage of development. Treated larvae were smaller in length and

depth, had more yolk, and less eye pigmentation than the controls (Figs. 11 and 12). Thus, UV-B irradiation retarded development in larvae and the extent of retardation was related to dosage. At the lowest dosage in our experiments ($63,000 \text{ J} \cdot \text{m}^{-2}$) length, body depth, eye pigmentation, and yolk diameter were different from the controls (t test $P < 0.001$) indicating a significant effect of UV-B irradiation on growth and development even at the lowest dosage.

The melanosomes in the melanophores of anchovy and mackerel larvae were dispersed in those exposed to UV-B radiation, whereas they were aggregated in the controls (Fig. 13). The extent of dispersion as indicated by our grading system increased with dosage. Melanosomes in the fully dispersed condition (grade 3, Fig. 5) occurred commonly at dosages at and above $90,000 \text{ J} \cdot \text{m}^{-2}$ and less commonly at lower dosages, but even at the lowest dosage ($63,000 \text{ J} \cdot \text{m}^{-2}$) pigment in anchovy melanophores was more dispersed than the controls (t test, $P < 0.001$).

The literature on effects of UV irradiation on pigment movement within melanophores of fishes is limited to effects of energy from germicidal lamps. In contrast to our findings, these studies indicate that UV irradiation at 254 nm induces some aggregation rather than dispersion of melanosomes (Fujii, 1973; Fujii *et al.*, 1973). In addition, Fujii *et al.* (1973) demonstrated that UV irradiation caused a depression of the response of the melanophore to pigment aggregating substances (norepinephrine and melatonin) which was proportional to dosage. They suggested the UV-induced inhibition of melanosome mobility was caused by UV-induced lesions in the neuro-effector system. To determine if the changes we observed in response to UV-B were reversible or were caused by neural damage would require further experimentation and submicroscopic analysis.

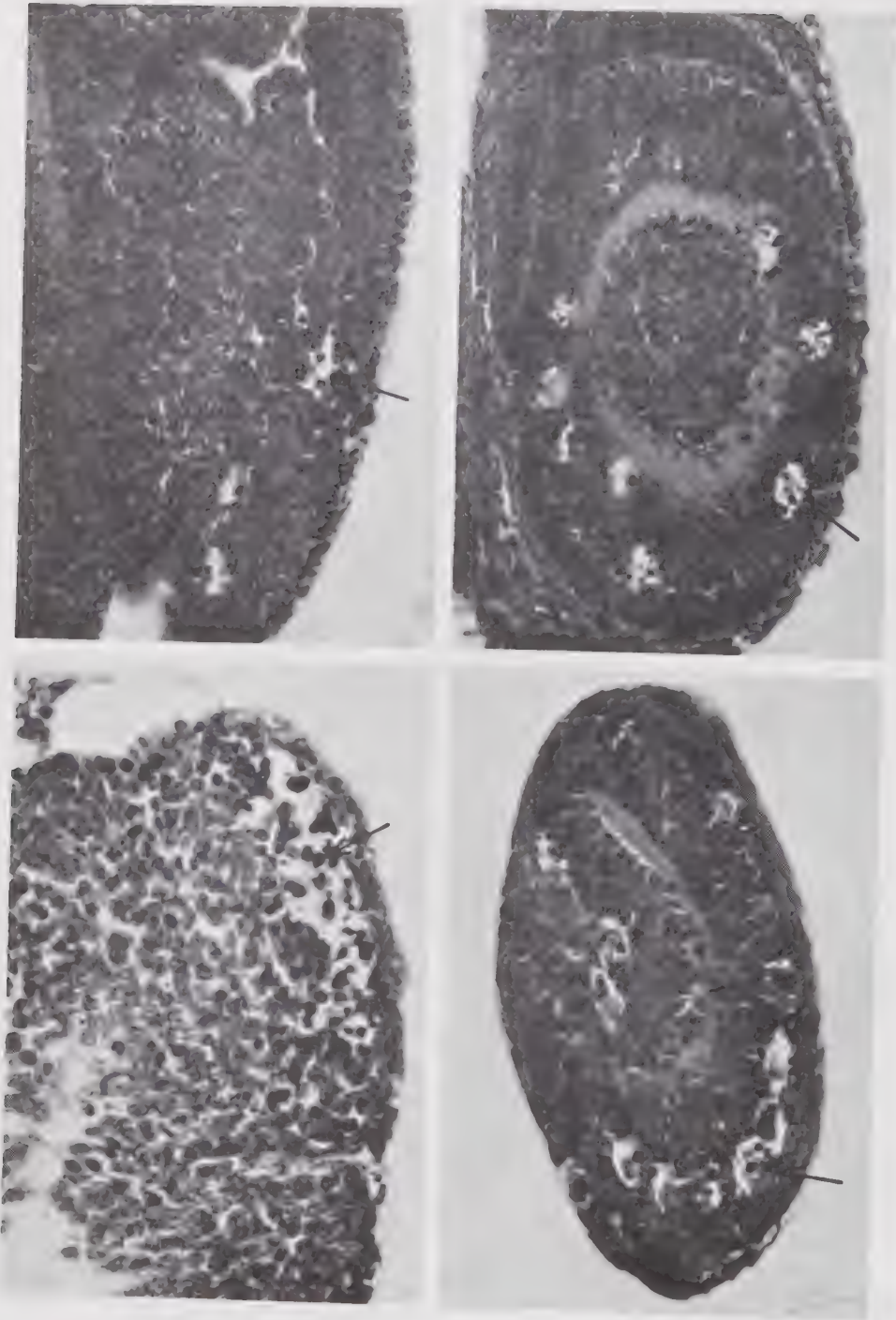


Figure 9. Eye (top left) and brain (top right) of northern anchovy larvae and eye (bottom left) and brain (bottom right) of Pacific mackerel larvae showing lesions (arrows) produced by UV irradiation with CTA filters. Irradiations were $109 \text{ k J} \cdot \text{m}^{-2}$ (top left), $115 \text{ k J} \cdot \text{m}^{-2}$ (top right), $199 \text{ k J} \cdot \text{m}^{-2}$ (bottom left), $199 \text{ k J} \cdot \text{m}^{-2}$ (bottom right). Sagittal sections stained with H and E, 400X.

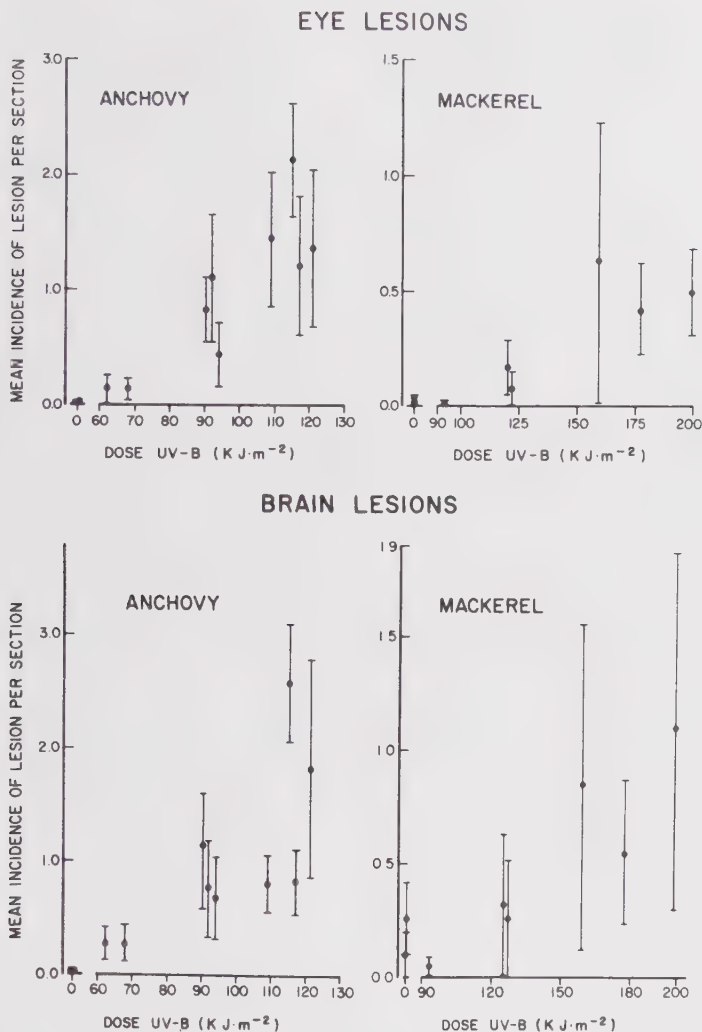


Figure 10. Mean incidence of lesions in the eye and brain of northern anchovy and Pacific mackerel larvae that survived various unweighted doses of UV-B irradiation. UV energy source was FS-40 lamps filtered by CTA; controls, ~0 UV-B, had Mylar filters; points are means for treatments, and vertical bars are two standard errors.

DISCUSSION

Our approach in these experiments was to simulate natural conditions and we did not evaluate photoreactivating repair of UV-induced damage. In the aquarium system white lights were turned on 2.5 h before and continued for 2.5 h after UV-B exposure (Fig. 4). The flux in the region for photoreactivation, however, was somewhat lower in the aquarium system than under natural conditions and this could have affected the results. That the DNA-weighted dose-response relation was about the same in experiments using natural solar irradiation supplemented

with UV (anchovy PS experiments) as in the aquarium experiments suggests that our results were not affected by the lower level of photoreactivating energy in the aquarium system.

A striking feature of these results was the occurrence of marked and clearly defined damage after an exposure of only 4 days. The damage included lesions in the brain and retina, marked retardation of growth and development and abnormal dispersion of melanosomes. Significant damage occurred not only in those larvae surviving a 50% mortality dose but in the survivors of all dosages. It seems unlikely that any of the damaged survivors, regardless of dosage, would

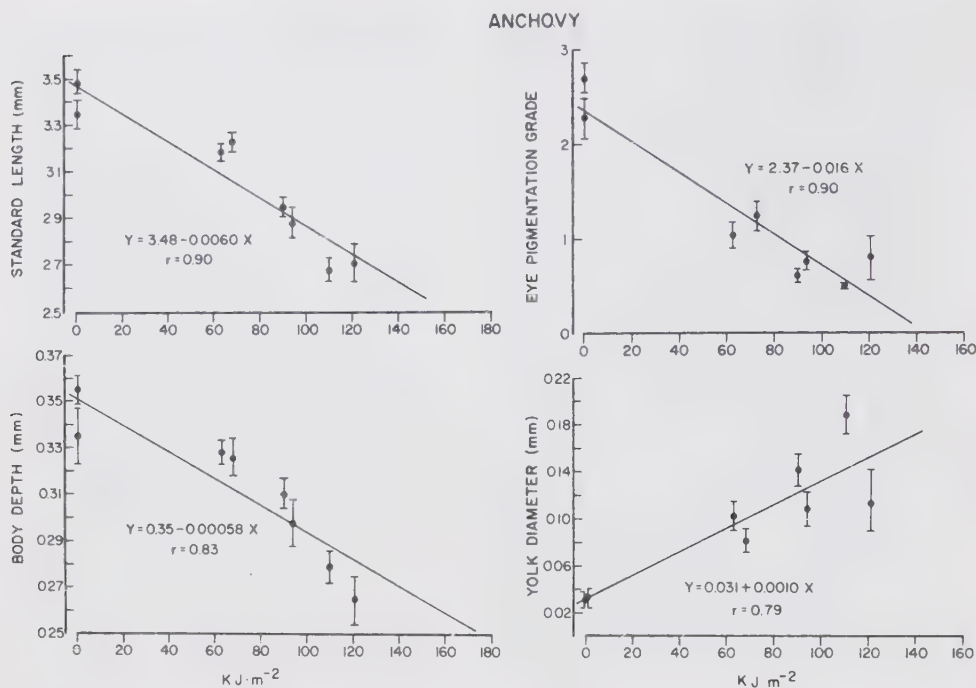


Figure 11. Standard length, body depth, eye pigmentation grade, and yolk diameter of larval northern anchovy surviving various doses of UV-B (FS-40 lamps, CTA filters). Mylar-filtered controls are shown as ~0 dose; points are treatment means; and bars, two standard errors.

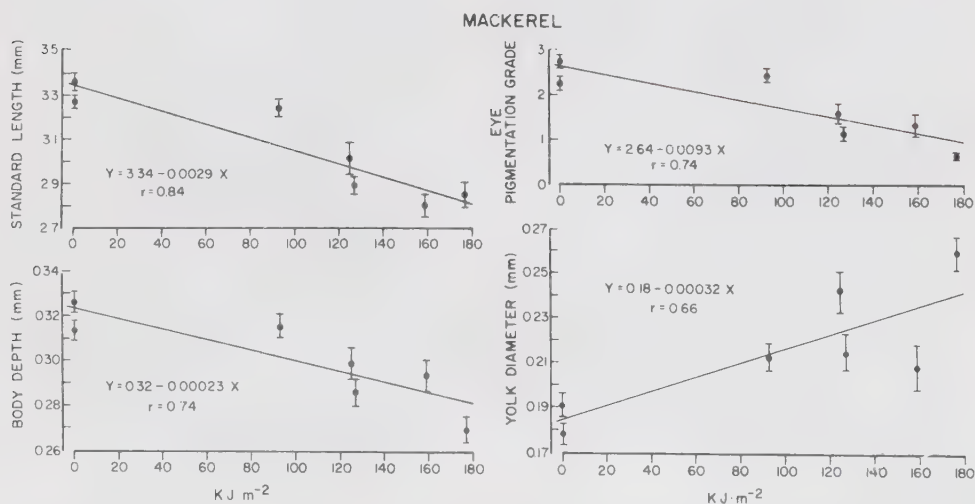


Figure 12. Standard length, body depth, eye pigmentation grade and yolk diameter of larval Pacific mackerel surviving various doses of UV-B (FS-40 lamps; CTA filters). Mylar filtered controls are shown as ~0 dose; points are treatment means; and bars, two standard errors.

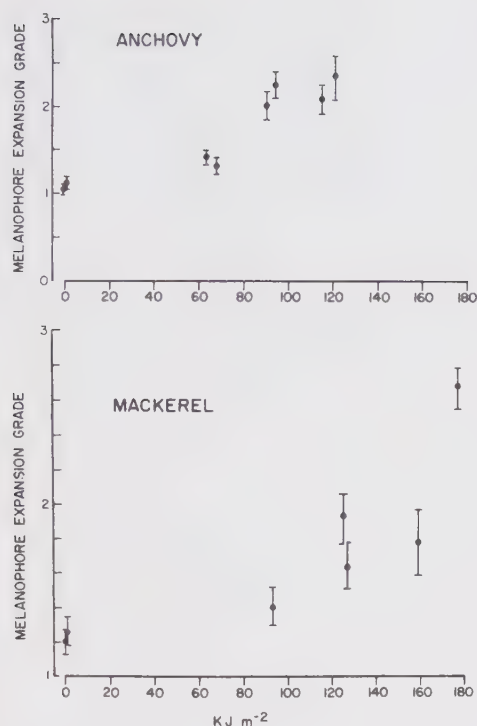


Figure 13. Relation between average melanosome dispersion grade and unweighted dosage in anchovy and mackerel larvae. Source of irradiation was FS-40 lamps with CTA filters. Mylar controls are shown as ~0 dose; points are means for treatments; and bars, two standard errors. Grade 1 is completely aggregated condition; and grade 3 completely dispersed (see Fig. 5).

be able to feed successfully. Retardation of development is another potential source of mortality under natural conditions because it prolongs the stage of highest vulnerability. Natural mortality in the sea during the embryonic period (egg through yolk-sac stages) is generally 3–10 times higher than after the larvae begin feeding (Jones and Hall, 1974).

We estimated from solar irradiance measurements made in September–November that the DNA weighted dose for 4 days in June in La Jolla would be $439 [\text{J}\cdot\text{m}^{-2}\cdot(4 \text{ day})^{-1}]_{\text{DNA eff.}}$, assuming the daily dose to be about six times incidence at solar noon. Assuming a 6% loss through the sea surface gives a value of $413 [\text{J}\cdot\text{m}^{-2}\cdot(4 \text{ day})^{-1}]_{\text{DNA eff.}}$ for the DNA weighted dose just beneath the surface. This estimate differed by only 2% from the value $422 [\text{J}\cdot\text{m}^{-2}\cdot(4 \text{ day})^{-1}]_{\text{DNA eff.}}$ calculated by Smith and Baker (in this issue) using Green *et al.*'s (1974) semi-empirical analytic formula with coefficients fit to multiscattering data to obtain the total daily dose just beneath the sea surface in mid-June at La Jolla for the "ambient" ozone depth of 0.32 cm. Thus, to relate our experimental results to effects of ozone depletion, Green's

analytic formula for downward spectral irradiance ($[\text{W}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}]$) was transmitted through sea surface, then weighted by the Setlow DNA action spectrum and integrated to obtain the biologically effective downward irradiance ($[\text{W}\cdot\text{m}^{-2}]_{\text{DNA eff.}}$). This result was then integrated, as a function of sun angle, over the course of a day and multiplied by four to obtain the total 4-day biologically effective dose ($[\text{J}\cdot\text{m}^{-2}\cdot(4 \text{ day})^{-1}]_{\text{DNA eff.}}$). These calculations, expressed as the total cumulative, Setlow DNA weighted, UV flux in $\text{J}\cdot\text{m}^{-2}$ for 4 days in June are compared to our results for anchovy below:

$[\text{J}\cdot\text{m}^{-2}\cdot(4 \text{ day})^{-1}]_{\text{DNA eff.}}$	Event
422	0.32 cm ozone ("ambient")
564	0.28 cm ozone (13% reduction)
758	0.24 cm ozone (25% reduction)
760	First incidence of lesions and retardation of growth in anchovy
1150	LD_{50} for anchovy
1434	0.16 cm ozone (50% reduction)

These calculations indicate that incidence of lesions and retardation of growth in anchovy larvae occur at dosages that could be expected to occur at the surface in 4 days in June at our latitude provided that the optical ozone depth is reduced about 25%. Fifty % mortality could be expected to occur at the surface in 4 days at a level between a 25 and 50% reduction. Smith and Baker (in this issue) have carried the calculations a step further and have estimated the DNA weighted dosage as a function of depth in the sea for various water types. Their calculations indicate that in clear ocean water a significant incidence of lesions and retardation of growth could occur only at the surface at a 25% reduction in ozone and down to 3.5 m at a 50% reduction. Eggs and larvae of anchovy commonly occur at these depths but an assessment of the potential damage to pelagic fish populations would require additional work. These estimates depend on the assumption that the Setlow DNA weighting function adequately expresses the relation between wavelength and dosage in anchovy, and on statistical and radiometric uncertainties.

It must be reiterated that our experiments to date apply only to the first 4 days of life; the fate of surviving larvae, particularly those who exhibit lesions, who must now begin to seek food and avoid predators, remains to be studied. If we assume that approximate reciprocity holds, as it appears to for the relatively short periods we have studied (4–5 days), then lower dosage rates over a longer time period could produce the same effects found at higher rates for a few days. The effects of long-term chronic dosage, must be evaluated as such studies probably would alter not only our present projections but could be of great significance in understanding the course of pathological changes induced by UV exposure. Induction of tumors might be one of the characteristic pathological changes revealed by longer term studies. For example, Hart and Setlow (1975) have shown that single exposures of cells of the fish *Poecilia formosa* to UV irradiation (254 nm) resulted in neoplastic transformation after 3–9 months.

The level of UV-B enhancement needed to produce structural anomalies and retard development argues for maintaining the integrity of the ozone shell. Whether or not the animals would or, in fact, could use evasive tactics (such as swimming deeper) is moot, and it is unlikely that adaptive evolutionary changes could be effected in time.

would have been impossible without the able and dedicated assistance of all members. Key individuals that we wish to thank include: Kathleen Dorsey, larval rearing, water chemistry, morphometric analysis; Robert Hundt, apparatus design and construction, radiometric measurement and calibration, and calculator programming; Beverly Macewicz, microtechnique and histological analysis. The cooperation of Raymond Smith and Karen Baker (University of California, San Diego) was also greatly appreciated.

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Implications of Multipurpose Fleets and Mixed Stocks for Control Policies¹

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Management of harvests from mixed stocks and multipurpose fleets requires the use of concepts not discussed in single species fishery models. Optimum harvest of a group of mixed stocks implies that an aggregate objective pertaining to the multispecies catch is maximized. This usually prohibits the attainment of the maximum sustained yield or the maximum economic yield for each individual stock. Operation of a multipurpose fleet is economically justifiable when there are significant annual or seasonal fluctuations in fish stock abundance. A simple linear model is developed in this paper to demonstrate how the multipurpose fleet can be a necessary part of rational management.

Key words: economics, management, multispecies

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Pour gérer la récolte de stocks mixtes par des flottilles polyvalentes, on doit faire appel à des concepts qui ne sont pas examinés dans des modèles de pêcheries d'espèces uniques. La récolte optimale d'un groupe de stocks mixtes suppose que l'on porte au maximum un objectif composite par rapport à des captures de plusieurs espèces. Pour cette raison, il est ordinairement impossible d'atteindre le rendement maximal soutenu ou le rendement économique maximal pour chaque stock. Il est économiquement justifiable d'exploiter une flottille polyvalente quand il y a d'importantes fluctuations annuelles ou saisonnières d'abondance des stocks. Nous élaborons dans cet article un modèle linéaire simple démontrant la façon dont une flottille polyvalente peut être partie nécessaire d'une gestion rationnelle.

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FISHERIES management science has not adequately addressed the problems associated with mixed biological stocks and multipurpose vessels. Both situations influence the economic and biological analyses required for optimization of the harvest. In the case of mixed stocks, the concept of maximum yield must be adapted to a multispecies aggregate rather than being applied on a stock-by-stock, or species-by-species basis. Economically desirable harvest rates for mixed stocks depend upon relative prices of the species caught and upon the costs of altering the species mix. In the first section below I review recent literature on mixed stock management and summarize the conclusions for fisheries policy.

Multipurpose vessels shift from fishery to fishery in response to seasonal fish abundance, closures by management, or fluctuations in prices and costs. Any economic or biological factors that cause economic returns to fluctuate can induce vessel operators to

diversify in an attempt to improve long run earnings potential or to decrease annual variations in income. Although economically irrational management methods may often be responsible for the appearance of multipurpose fleets, there are many situations in which investment in multipurpose vessels is justifiable. The examination of conditions favorable to multipurpose fleets and the determination of optimum size for a multipurpose fleet are the main subjects of the second part of the paper.

In developing an analysis of mixed stocks and multipurpose fleets, it was necessary to abstract from some of the more detailed problems of fishery regulations. Companion papers in this symposium by Adasiak (1979), Crutchfield (1979), Fraser (1979), and Scott (1979) draw more attention to the problems of regulating fisheries than I do. In particular, the cost minimization in the traditional economic efficiency approach to management requires that capital investment in fishing capability be limited. This requirement is often identified with license limitation programs, and I adopt this position in the discussion of optimum multipurpose fleet. The overinvestment may be transformed, however, from a problem of too many vessels to one of vessels that are too big or heavily equipped.

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Fraser is especially concerned that license limitation, and even restrictions on the total tonnage of the fleet, will not satisfactorily constrain the investment in fishing vessels and gear. Rather than repeat the arguments presented elsewhere, I refer the reader to the other papers in the symposium. In general, the whole spectrum of regulatory methods discussed in these other papers is applicable, with modification, to multiple stocks and multipurpose fisheries.

Management of Mixed Stocks

Several investigations of mixed stock fisheries have appeared in recent years. Among these are Anderson (1975, 1977), Clark (1976), Hilborn (1976), Hobson and Lenarz (1977), and Paulik et al. (1967). The papers by Hilborn and Paulik et al. treat the specific problems associated with mixed stocks of salmon. Conditions characterizing the salmon management problem are (1) the thorough mixing of many substocks of economically identical fish at sea, (2) the inability of fishing vessel operators to avoid the contemporaneous harvest of fish from more than one stock, and (3) the lack of biological interactions which affect the productivity of the individual stocks. All the other authors identify several categories of mixed stock fisheries. Hobson and Lenarz (1977) seem to have the most comprehensive taxonomy of mixed stock fisheries. Fish stocks may be ecologically interactive or not, and fishing gear utilized in the fishery may be flexible or inflexible.

The first characteristic, degree of interaction among stocks, depends upon the relationship of species in a food web. Stocks of predator fish may be food limited, thus implying a positive relationship between the number of predators and the size of the prey stocks. Two species may compete for food, in which case the size of one stock may be inversely related to the size of the competing stock. Finally, the several stocks being exploited may be neither competing for a common food source nor preying on each other.

The flexibility of the gear in targeting upon a single species or a subgroup of species depends upon both the physical characteristics of the gear and upon the spatial and behavioral attributes of the fish. When fish from several stocks are essentially identical as in the salmon fishery, the fishermen may realistically be assumed to have no practical means of discriminating among the several stocks available at a given time and place. Fishing gear that sweeps a given area is generally less selective among fish species or stocks than gear that requires that a target species have a particular physical or behavioral attribute. Trawl nets are perhaps the archetypical example of sweeping gear. Pacific halibut, for example, are taken in conjunction with a variety of other flatfish species by bottom trawlers. Longline gear, on the other hand, can discriminate against the smaller flatfish species because a larger hook prevents smaller fish from being caught.

Adding to this complexity is the great variability in species mix that any given gear type can achieve by selection of temporal and spatial deployment. At different times of day or in different seasons of the year, the species available to trawl gear differ radically. Also, a given species can mix with another species during certain life stages but not during others. In all of the published papers on management of mixed stocks, this richness of detail is sacrificed to the analytical tractability of the models. Those generalizations that I find promising for mixed stock management policy are discussed under the following two headings: (1) optimum harvest rates and (2) the incidental catch problems.

OPTIMUM HARVEST RATES

Existing analyses all seem to agree on one important aspect of the joint harvest problem. When the fishing gear used to harvest one or more mixed stocks is incapable of targeting upon single stocks, it is agreed that (1) the maximum harvest rate for the aggregate of stocks will be less than the sum of the theoretical maxima of the individual stocks, and (2) the less productive stocks will have to be reduced to levels that cannot support their individual maximum yields, and the more productive stocks will be exploited at rates close to, but generally less than, the individual stock maxima. Some stocks may even be driven to extinction by an aggregate sustained yield maximizing policy. This result leans heavily on two key assumptions: (1) that maximum physical yield is the objective, and (2) that the gear is inflexible. Different objectives and more flexible gear lead to different conclusions.

Preservation of genetic diversity, for instance, may be an important consideration. This particularly concerns biologists studying the effects of heavy exploitation of salmon stocks. From an economic standpoint, genetic diversity may have great value if it preserves future options and acts to increase overall productivity over time. Another major consideration is the relative economic values of the mixed species. For salmon this may not be of critical importance, but in groundfish harvests there are often high-valued species of relatively low productivity or great vulnerability mixed with larger stocks of lower-valued species.

Both Anderson (1975) and Clark (1976) derive conditions necessary for the economic optimization of mixed stocks. The value to be maximized is the aggregate sales value of the mixed catch minus the harvest cost. Just as in the single species models popularized by Gordon (1954) and Schaefer (1957), the economic optimum is examined by converting the physical yield curve into a value curve measured in dollars. When a two-species harvest is introduced, the economic value curve has two local maxima. The annual net economic yield is maximized when the marginal cost of fishing just equals the marginal sales value of the mixed catch. Since there will generally be two rates of harvest satis-

fyng this condition, the overall economic optimum occurs at the point that has the higher total net value. From a theoretical standpoint this is all that is needed. In practice, however, the aggregate biological yield is difficult to determine, especially when the two stocks being harvested interact biologically. Also, unlike the "biological" maximum, the economic optimum will not necessarily sacrifice the less productive stock to fully exploit the more abundant stock. If the smaller, more vulnerable stock has an extremely high value relative to the more abundant stock, the economic optimum may well dictate a low rate of exploitation which protects the small stock and leaves the large stock relatively underexploited.

Flexibility of the gear in targeting on individual species may provide a means to avoid retarding the development of a larger fishery to protect a small, high-valued stock. Flexibility implies that the relative harvest rates of mixed stocks can be adjusted by gear modification or targeting, while overall exploitation rate is controlled, as usual, by the total amount of fishing. For each possible relative rate of harvest of two species there will be a theoretical economic yield curve with two peaks. If it is assumed that the unregulated fishing vessels adopt those fishing methods that yield the greatest net revenue, then any alteration in fishing methods will result in an apparent reduction in earnings or increase in costs. But a regulated modification of relative harvest rates may result in a long-term increase in total sustainable economic yield. An optimal adjustment of relative harvest rates requires that the rate of increase in fishing costs be balanced at the margin against the rate of increase in equilibrium value of harvest.

INCIDENTAL CATCH PROBLEM

Among the most difficult and frequently occurring problems in fisheries management is the incidental, or by-catch problem. The general approach to mixed stock management discussed above does not include any mention of incidental catches simply because we assume that managers accept the mixed catch and optimize over the range of possible relative and aggregate rates of fishing. Under the multiple species approach, incidental catch is not a problem or nuisance. In what sense, then, can an "incidental catch problem" occur? It seems to me that the problem has two sources: (1) institutional or political inflexibility in setting objectives, and (2) technological and enforcement shortcomings.

If managers are committed to manage on a species-by-species basis, then each fishery management unit may become a proponent for the particular group of fishermen and gear types that specialize on its species. Each species management group will want to promulgate as many direct controls (gear regulations, season and area restrictions, and incidental catch allowances) as are necessary to protect its species and to maximize

the yield from its species. Under this sort of management institution it will be very difficult for any central authority to adopt a rational aggregate approach to the mixed stocks. Not only will the scientists studying each species develop a narrow viewpoint, but the operators in each separate group are likely to become a political force supporting the continuation of the enforced separation of fisheries. There will be no special interest group to protest the onerous economic costs that such a system will impose on society as a whole.

It must be admitted, however, that appropriate mixed-stock management procedures will not necessarily accomplish the ideal relative harvest rates without imposing incidental catch regulations. It is possible, for instance, that catch of some depleted but high-valued species should be prohibited. If this conclusion is economically rational, it is implied that there is some technological means of avoiding the prohibited species at reasonable cost. Economists often recommend the use of tax incentives to encourage desired behavior or discourage undesired behavior. When the behavior (or fishing technology) occurs outside the manager's observation range, however, it may be impossible for a tax or fee system to work. Obviously, the incidental catch can be discarded at sea while the economic rewards and/or penalties are applied at the point of landings. Control over fish landings, therefore, is unlikely to provide adequate protection to a prohibited species.

Once it is concluded that landings regulations or taxes cannot enforce the desired fishing rates, other direct regulations may be considered. The imposition of any kind of gear requirement, or season or area restrictions, should be preceded by a demonstration that the long-run increase in potential catch value exceeds the increase in harvest costs. In conclusion, the problem of regulating incidental catches can arise in rational mixed-stock management programs, but the frequency of such problems would probably be greatly reduced if multiple species management approaches were adopted.

Management of Multipurpose Fleets

Despite its relevance to fisheries management, multipurpose vessel operation has been subject to few penetrating analyses. Meany (1977) has recently written one of the few overviews of the pertinent issues. Five reasons for fishermen to invest in multipurpose capability are identified by Meany. These are (1) changes in relative abundance of different species, (2) changes in relative prices of species, (3) seasonal factors, (4) differential changes in gear costs, and (5) personal preference of the skippers. Like any successful businessman, the fishing vessel owner must periodically assess the profitability of various production methods. When conditions change, the profitability of fishing changes, and the fishermen must adapt.

Meany goes on to develop a hypothetical scenario involving successive imposition of limited entry to four interrelated fisheries. All vessels with historical participation in a given fishery are issued licenses to fish in that fishery. Over time this results in unequal treatment of newcomers who can fish only in the less-developed fisheries. As more fisheries become heavily exploited, they are put under license limitation programs. Eventually, a bewildering array of single and multiple fishery licenses emerges. Under this system of limited entry there is far too much potential effort for some species (due to the inclusion of all past participants), while at the same time some vessels have too little flexibility in fishing methods to survive the inevitable failures of recruitment in individual stocks. The system, in other words, protects neither fish stocks nor fishermen. Meany's conclusions for fishery management are (1) multipurpose fleets should be managed as a unit by limiting access to the multi-species group of fisheries; (2) the optimum number of vessels in the group should be determined in accordance with maximum sustainable yield, maximum profit, or some other socially acceptable objective; (3) changing conditions imply changes in the optimum fleet size and managers should be prepared to increase or decrease the fleet size; (4) differential license fees should be introduced for each fishing method to shift effort from the more heavily exploited to the less heavily exploited fisheries; and (5) licensing regulations can be supplemented, if necessary, by gear restrictions and other forms of catch regulation. Under this recommended system, fishermen are free to decide (subject to fees and gear restrictions) which of the fisheries they will enter during any given year.

Implementation of an economically rational management program of the type that Meany recommends will depend crucially upon the ability of the managers to determine the optimum fleet size. This will be true regardless of which regulatory methods are adopted. To examine how one might accomplish this task, I have developed a simple two-stock model. I assume that the two essential aspects of economic rationalization, regulation of the catch and regulation of long-term commitment of resources to fishing and processing capital, are separable. Although optimum extraction rates and optimum capital stock can be derived formally from a single optimizing model (see Clark 1977; Anderson 1975; Smith 1969), separation of the two problems has practical value. Rates of exploitation will often be determined through intensive interaction among biologists, economists, fishermen, and managers. Any proposals for further regulation aimed at cost minimization will be developed largely by economists. Controls on fleet size, therefore, are in practice often appended to some preexisting plan for controlling catch.

The discussion of optimum fleet size is developed in two parts. In both, the annual allowable catches are assumed to be interpreted as fishing quotas which are en-

forced through season closures. Under Case I, it is further assumed that the annual quotas are fixed and recurring year after year. Case II examines the implications of random variation in the fish stocks which is reflected in annual variation in the two quotas.

CASE I—FIXED ANNUAL QUOTAS

The two fish stocks may be potentially available to the fishing fleet throughout most of the year or they may be available in two discrete seasons due to natural variations in availability. In either case the development of a two-stock fishery can be examined by reference to Fig. 1. A fuller algebraic development of the model is contained in the Appendix. Only a verbal explanation will be attempted in the main text. In both panels of Fig. 1 the number of vessels in the fleet is measured along the horizontal axis.

In the upper panel the curve labeled R represents the level of revenue minus operating costs earned per vessel. As the number of vessels is increased the net operating revenue, R , proceeds through three stages. As N increases from zero up to the number required to fully utilize the quota of the more profitable stock (assumed to be stock 1), the profit per vessel remains constant. If the two stocks are available all the time, then until the number of vessels exceeds N^* , no vessels fish the less profitable stock. Only stock 1 is fished because the quota is taken at a slow enough rate to allow full utilization of the fleet. If the fishing vessels are earning sufficient profits to attract additional fishermen into the fishery for stock 1, however, the fleet will continue to expand. As the number of vessels expands beyond N^* , the net revenue per vessel declines because each vessel must stop fishing for the more profitable stock 1 when the quota is reached. An increasing fraction of the available fishing capacity will be devoted to the less valuable second stock.

With free access to the hypothetical fishery the eventual size of the fleet is determined by the prospective profits and the capital costs associated with owning a fishing vessel. It is usually realistic to assume that additional fishing vessels will be built to enter the fishery until the prospective net earnings (revenue minus operating costs) are just balanced by the annual capital costs. The line labeled I_1 in Fig. 1 represents a level of capital cost that implies an eventual fleet size of N_1 . If capital costs are at the lower level represented by the line I_2 , the fleet will expand further to N_2 . When the number of vessels reaches N^{**} , both quotas will be taken in a full fishing year. And further expansion of the fleet beyond N^{**} causes all vessels to remain idle for the remainder of the year. Clearly, this simple model could be expanded to allow for a third or fourth fishery which would be entered successively as the fleet grows and fishing seasons for the more profitable stocks become shorter and shorter.

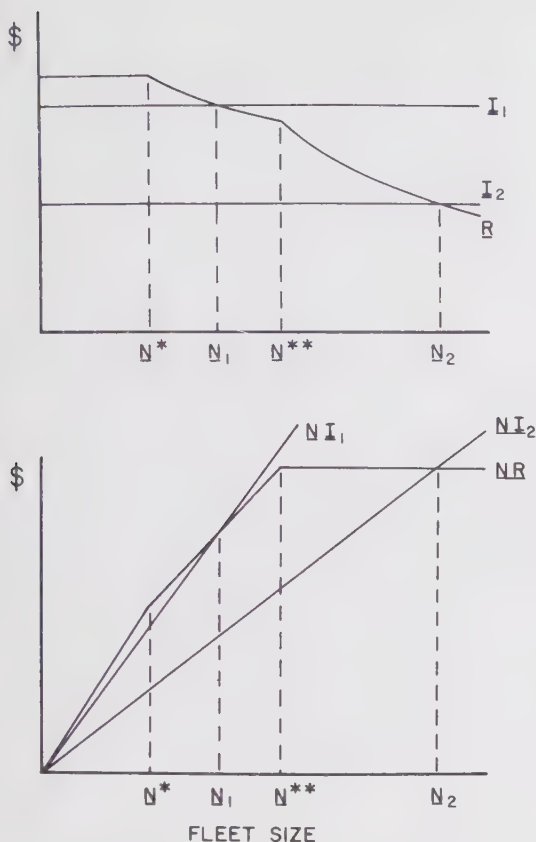


FIG. 1. Theoretical relationship between fleet size (N) and net earnings per vessel (lower panel), and between fleet size and total profits (upper panel), for two stocks of fish.

The economically rational fleet size depends upon the total net earnings of the fleet and the total commitment of capital. The relevant diagram for this examination is in the lower panel of Fig. 1. The curve labeled NR represents the total fleet earnings in excess of operating costs, and the two lines NI_1 and NI_2 represent the total capital costs corresponding to per vessel capital costs I_1 and I_2 . The maximum net earnings of the fleet in excess of capital costs occurs at the fleet size that obtains the greatest vertical distance between NR and NI . For capital cost I_1 the optimum fleet size is N^* , a fleet just large enough to fully exploit the more profitable stock. With the lower capital cost, NI_2 , the optimum fleet, N^{**} , is just large enough to take both of the quotas. The simple logic of this is that an economically rational management program cannot allow the fleet to expand further after the incremental increase in capital cost exceeds the incremental increase in net earnings.

Suppose the management program begins to seek eco-

nomically efficiency only after the fishery has already reached the free-access equilibrium fleet size. If the capital cost curve NI_1 applies, then the fleet size will be N_1 , and an excess number of vessels, equal to N_1 minus N^* , will be already in the fishery. Unless the vessels can be transferred into an alternative, underdeveloped fishery, however, it will not be desirable to initiate a licensing program for only N^* vessels. Unlicensed vessels either will go bankrupt or will suffer a capital loss. A similar conclusion holds if the capital cost per vessel is I_2 .

In the fully developed free-access fishery it will be apparent that vessels must participate in more than one fishery to earn a satisfactory return on investment. But it is also clear that the fleet may not need to be multipurpose if it were not overbuilt. This is certainly the case if the two fisheries are not seasonal. The vessels become multipurpose only after the fleet is larger than necessary to fish stock 1. With capital cost I_1 , the fleet need be no larger than N^* , and no vessels need to shift into stock 2. With capital cost I_2 the fleet needs to be no larger than N^{**} , and the manager can create two separate fleets that specialize on the two stocks. Thus, without seasonality in the fisheries, none of the reasons for diversification identified by Meany (1977) exist. By licensing two separate fleets, the management program can ensure that each fishing season is as long as possible, thus decreasing the costs of processing and storage facilities onshore.

If the two stocks have natural seasons, however, and the capital cost is low enough to justify full exploitation of both quotas, the manager may as well license all of the N^{**} vessels to fish both stocks. This is true at any rate if the cost of building an optimum size multipurpose fleet does not exceed the cost of building two specialized fleets. With a multipurpose fleet, none of the vessels will be forced to spend part of the year in idleness. Thus, the economic rationality of multipurpose fleet with fixed prices, costs, and annual quotas depends upon whether the fish stocks are seasonally available and whether the cost of building multipurpose capability into the vessels is excessive.

The main management implications to be gleaned from the fixed quota model are summarized as follows:

- 1) A multipurpose fleet is economically efficient if it is just large enough to fully exploit all stocks that yield sufficient net revenue to cover capital costs on an annual basis.
- 2) If the two stocks can support separate fishing fleets by virtue of year-around availability of fish, then it may be preferable to maintain two distinct fleets through regulation. It should also be recognized that all vessels licensed to fish only for the less profitable stock will be unhappy with this circumstance.
- 3) If only one stock is profitable enough to support a separate fleet in specialized fishing, then it is economically optimal to have a fleet just large enough to fully exploit one stock. This may appear wasteful or

paradoxical to those who wish to see every fish stock fully utilized.

4) If the fisheries must occur during separate seasons and if it is reasonably inexpensive to outfit vessels for multipurpose operation, then the fleet should be licensed to fish both stocks. Since the full utilization of one of the quotas is likely to require fewer vessels than the other, the multipurpose fleet will have excess fishing capability. But if economic conditions dictate that both stock quotas be fully utilized, the appearance of excess capability is not wasteful.

Under the conditions of the two-stock, fixed quota model, there are only two reasons for having a multipurpose fleet rather than one or two specialized fleets. First, a multipurpose fleet is more economical when the fisheries are naturally seasonal in character. And second, economic rationalization of an already over-capitalized fleet may allow for continued operation of multipurpose vessels to maintain their economic viability as private businesses. This second rationale is not a long-term policy, but rather a condition to be countenanced during a transitional period. The length of the transitional period depends upon the life of the capital equipment in the fishery. As vessels depreciate to the point of nonprofitability, they should be retired.

CASE II — VARIABLE ANNUAL QUOTAS

Environmental influences can cause uncontrolled variations in stock sizes which in turn elicit annual variations in catch rates and quotas. Assuming that prices and fishing costs are fixed, the variations in catch rates translate directly into variations in net revenue earned per day of fishing. The relative profitabilities of two stocks will switch occasionally. Thus each of the following four circumstances may occur in some years: (1) each stock yields some positive net revenue to fishermen, (2) neither stock yields net revenue, (3) fish stock 1 is sufficiently abundant to yield net revenue but stock 2 is not, and (4) fish stock 2 yields net revenue but stock 1 does not. Since neither of the stocks can be relied upon to support a fishing fleet every year, it is natural to suspect that a multipurpose fleet would be more profitable than two specialized fleets.

To illustrate how the optimum fleet size may be affected by variability of quotas and catch rates, I have developed a numerical example the pertinent characteristics of which are listed in Table 1. It is assumed that each stock has five possible annual quotas that occur with known frequencies. One tenth of the time, for instance, the annual quota for stock 1 is zero; 24% of the time the quota is 10 000; 32% of the time the quota is 20 000; and so forth. Similar conditions are specified for stock 2. Fish from stock 1 are sold for a price of \$10, while fish from stock 2 bring a price of \$20. A day of fishing is assumed to cost \$70/d regardless of which stock is being fished.

To complete the example, I assume that each vessel

TABLE 1. Characteristics of the 2-stock multipurpose fleet model with variable annual quotas and catch rates.

	Quota	Catch rate	Relative frequency	Net revenue/d fishing
Stock 1	0	10.0	0.1	—
	10 000	12.5	0.24	55
	20 000	15.0	0.32	80
	30 000	17.5	0.24	105
	40 000	20.0	0.1	130
Stock 2	0	15.0	0.1	—
	20 000	22.5	0.24	42.5
	40 000	30.0	0.32	80.0
	60 000	37.5	0.24	117.5
	80 000	45.0	0.1	155.0

is able to fish 200 d/yr and that the annual capital cost per vessel is \$8 thousand. Given the relative frequencies and net daily earnings corresponding to the various quotas listed in Table 1, the expected annual net revenue per vessel and expected annual fleet profits can be computed for any given fleet size. The computations were performed for each stock assuming that no vessels are allowed to change fisheries. Table 2 summarizes the results.

If the two stocks of fish are to be harvested by two separate fleets, then expected net earnings before capital cost per vessel falls in each fishery as fleet size increases. This relationship is comparable to that derived in Case I for a fixed annual quota. As indicated in Table 2, the average net annual earnings per vessel falls to about \$8 thousand when each fleet expands to 14 vessels. Thus

TABLE 2. Relationship between expected annual profits and fleet size for two separate fishing fleets.

Fleet size (N)	Stock 1		Stock 2	
	Vessel net earnings (R)	Fleet profits (NR)	Vessel net earnings (R)	Fleet profits (NR)
4	15.4	29.6	15.9	31.6
5	14.9	34.8	15.7	38.6
6	14.7	40.0	15.5	44.7
7	14.2	43.1 ^a	15.0	48.8 ^a
8	13.2	41.9	14.1	48.6
9	12.3	38.9	12.8	43.4
10	11.3	33.5	11.5	35.4
11	10.3	25.5	10.5	27.4
12	9.5	17.5	9.6	19.4
13	8.7	9.5	8.9	11.4
14 ^b	8.1	1.5	8.2	3.4
15	7.6	-6.5	7.7	-4.6

^aMaximum expected fleet profits.

^bMaximum fleet size which returns, on the average, the annual capital costs.

a free access fishery might stabilize at 14 vessels per fishery, or 28 vessels overall. I say might because vessel owners will not necessarily evaluate the probabilities of earnings the way that an "objective" fishery manager does. Defining an optimum fleet as one that maximizes the expected annual profit earned, the optimum fleet size for stock 1 is seven, and for stock 2 is seven. The aggregate profit earned on the average from both stocks is \$91.9 thousand and is generated by a total fleet of 14 vessels.

To investigate the economic consequences of the alternative policy of allowing vessels to shift from one stock to the other whenever profitable, the probabilities of encountering combinations of stock quotas must be specified. Three alternative bivariate relative frequency (or probability) distributions are introduced for this purpose. The first assumes statistical independence of the two stocks. This requires that the probability of encountering any given combination of two quotas be equal to the product of the probabilities of each quota. Thus the probability that both quotas will be zero in any year is $0.1 \times 0.1 = 0.01$. By constructing the joint probabilities in this fashion, the marginal probability of any single quota is the same as specified for the separate quotas in Table 1. Comparability of the multipurpose and specialized fleet examples is thus preserved.

It is assumed that each vessel fishes the more profitable stock until the quota is reached. If the other stock is also profitable, then each vessel switches fishing modes and continues fishing until either (1) 200 d of fishing accumulate, or (2) the second quota is reached. The expected annual net revenue per vessel is calculated by multiplying each of the 25 possible net revenues by the corresponding probability from the joint probability matrix. Expected annual profit equals the expected net revenue minus the capital cost. Additional details regarding the computation of expected net revenue, including a listing of the probability matrix, are in the Appendix. The results of the expected value computations are displayed in Table 3.

The optimum fleet size for statistically independent stocks is 13 vessels. The corresponding fleet profit is \$105 thousand. In comparison to separate fleets, the multipurpose fleet is smaller, thus saving capital costs, and achieves a greater average net revenue per vessel. This result depends upon the fact that multipurpose vessels can fish stock 2 when stock 1 is low, and stock 1 when stock 2 is low. It should be expected, therefore, that the economic advantage of multipurpose vessels should depend upon the assumed relationship between the two stocks. If the two stocks are negatively correlated, there should be greater opportunity to shift from stock to stock. If the two stocks are positively correlated, less economic advantage will be enjoyed because when one quota is large the other is also likely to be large.

The expected annual fleet profits with positive and negative correlation between stocks are listed in col-

TABLE 3. Relationship between multipurpose fleet size and annual profits earned from the fishery.

Fleet size (N)	Annual fleet profits with		
	Independent stocks	Negatively correlated stocks	Positively correlated stocks
	(1000's)		
4	48	52	43
6	71	78	63
8	91	101	80
10	101	112	90
11	103	114	93
12	104.7	114.9 ^a	96
13	105.3 ^a	114.6	98.1
14	104.0	111	98.4 ^a
15	102	107	97.6
16	98	100	95

^aProfit maximum.

umns 4 and 5 of Table 3. The optimum fleet size is smaller when stocks are negatively correlated, just as expected, and the multipurpose fleet is more profitable. With positive correlation between stocks a larger fleet is required to maximize profits, but, perhaps surprisingly, the multipurpose fleet is still more profitable than separate fleets. In general, therefore, the greater the negative correlation between stocks, the more attractive is the use of a multipurpose fleet.

If the price of fish from stock 2 in the numerical example is reduced from \$5 to \$3, then the expected annual net return from a separate fishery on stock 2 becomes negative. In this situation it is not possible to maintain a separate fleet for stock 2, but it is still useful to allow the fleet fishing stock 1 to fish for stock 2. With the lower price for stock 2, the optimum fleet for a separate stock 1 fishery is 7 vessels yielding an average of \$43 thousand in profits annually. In contrast, a multipurpose fleet would be 9 vessels with an aggregate expected profit of \$58 thousand. It is conceivable that a fleet could thrive on a group of fluctuating stocks, no one of which yields a positive expected annual profit. Limited entry for a single stock under such conditions would be inappropriate, because no specialized fleet would be economically viable.

Other important considerations not introduced in the example are (1) the cost of specialized gear and/or the cost of shifting from one stock to the other, (2) enforcement or monitoring costs associated with multipurpose fleets, and (3) the economic loss associated with shorter fishing seasons under multipurpose fleets. Any one of these three could, upon incorporation in the analysis of optimum fleet size, reverse the decision in favor of multipurpose fleets. In the numerical example, the multipurpose fleet was expected to earn \$14.1 thousand more in annual profits than could separate, specialized fleets when the stocks are sta-

tistically independent. If it costs more than \$14.1 thousand to outfit 14 vessels for multipurpose fishing rather than for specialized fishing, then specialized fishing is preferable. Also, it is conceivable that enforcement of regulations, when vessels shift from stock to stock during a year, could be more expensive or cumbersome than when vessels are specialized. If enforcement costs are to be considered in the design of management programs, separation of vessels into specialized fleets may be economically desirable. Before this conclusion is reached for any specific case, hard data and analysis should demonstrate that enforcement costs with multipurpose fleets exceed benefits. Simple administrative ease should not be taken as a compelling case for separate licensing by species or by geographical area.

As noted in the discussion of the fixed annual quotas, fishing seasons may be longer with specialized fleets than with a multipurpose fleet. This would be true if the multipurpose vessels deploy solely on the more profitable species first and then shift to less profitable species. In some cases (salmon runs being one example), the time period over which the fish are available to the fleet may be very short in any case. Nevertheless, some fisheries can be unnecessarily forced into a short time span by the operation of a multipurpose fleet. An examination of the processing and storage costs should serve to determine whether these costs exceed the potential benefits of multipurpose fleet operation.

Management implications of the variable annual quota model are

- 1) Multipurpose fleets are an economically rational response to economic and environmental variability. The ability to shift from species to species is beneficial to vessel owners and can be important to the economic optimization of a fishery.

- 2) Since profits per vessel fluctuate, any fees charged to inhibit entry or to extract rents for the public treasury should be flexible. Annual license fees, for instance, should not be fixed at a level that causes hardship to vessel owners in years of poor fishing. Large fixed fees could be replaced by landings taxes or royalties that fluctuate with the fishery.

- 3) With multipurpose fleet management, there will be apparent excess effort for at least one of the stocks in most years and excess effort for all stocks together in some years. Management of harvest rates must rely upon annual quotas or some other control besides fleet size. Limited access simply provides some long-run average control over effort.

This last point is of particular interest because it suggests the real problems that will crop up in any attempt to identify overcapitalized fisheries or to measure the degree of overcapitalization. Examination of economic data from 1 or a few years may be insufficient to determine whether overcapitalization has occurred. As a corollary, rapid changes in limited entry policies are

unlikely to be correctly evaluated. None of this, however, weakens the basic conclusion that free-access fisheries will tend to overinvest in vessels and gear, and that economic efficiency will occur only under a management scheme that limits investment.

Conclusions

Several implications for economically rational control of mixed stocks and multipurpose fleets were developed. It was concluded that mixed stock management requires that individual species objectives be abandoned in favor of aggregate yield objectives. Optimum harvest rates must be developed with full accounting of the revenue and cost effects on all species being harvested. Regulation of fishing methods or gear will influence the relative harvest rates of two or more mixed stocks. Thus, incentives such as differential landings taxes, or standards such as gear or area restrictions may appear prominently in the list of regulatory tools for mixed stock management. Although it is suspected that a multispecies management approach will largely avoid the creation of "incidental catch problems," it is difficult to reach any general conclusions. More detailed investigation of specific cases will undoubtedly reveal conditions under which combinations of regulatory controls will be optimal.

Multipurpose vessels are shown to be a reasonable response to variations in underlying biological or economic conditions. A vessel capable of fishing in several discrete fisheries is like a diversified portfolio; it is exposed to less financial risk. Furthermore, when two or more fluctuating fish stocks can be harvested by a common fleet, economic efficiency may require that the fleet be managed as a multipurpose fleet. Specialized fleets are efficient with stable, year-round fisheries, but few fisheries fit this description. Thus, the presumption is that license limitation on a species-by-species basis is to be avoided. As a consequence, short-term regulation of harvest rates must be achieved by more flexible methods such as landings taxes, quotas, season or area closures. Management of investment in fleet capacity simply provides the necessary long-term control over capital costs.

Both the biological and economic conditions underlying multispecies fisheries present vast problems for future research. Ecological models for fishery management may need to specify more precisely the effects of predator-prey linkages or competition for food among stocks. An alternative approach suggested by Dickie (1973) is to develop more aggregated models that emphasize harvesting fish of a given size or at a given trophic level rather than individual species. Economic analyses required to make a multispecies model operational include studies of market pricing, processing requirements and costs, gear flexibility, and fishing cost functions. Although it suggests some important concepts for management, the multipurpose fleet analysis

developed above must be considered provisional and incomplete. Clearly, many vessels operate in several fisheries; it will be difficult in practice to isolate a fixed fleet of vessels fishing a closed set of stocks. Because of differences in cost, varying seasonal and market conditions, and discontinuities in stock abundances, the appropriate grouping of species will be different at different times and places. Extension of the multipurpose fishery model to include complex overlapping species groups may prove useful. It is hoped that this paper encourages further research along these lines.

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Appendix

The following notation is adopted for the model:

- P_1, P_2 Market prices for the two species.
- C_1, C_2 Daily fishing costs per vessel when fishing for species 1 and species 2.
- T Amount of fishing time per year per vessel (e.g. 200 d).
- I Annual capital cost per vessel.
- t_1, t_2 Number of days that vessels fish for species 1 and 2, respectively (note: $t_1 + t_2 \leq T$).
- Q_1, Q_2 Annual quotas for the two species.
- X_1, X_2 Daily catch rates for species 1 and 2.
- N Number of multipurpose vessels in the fleet.

The net daily operating revenue per vessel in each fishery is

$$(1) \quad r_i = (P_i X_i - C_i), \text{ for } i = 1 \text{ or } 2.$$

Annual net operating revenue per vessel is

$$(2) \quad R = r_1 t_1 + r_2 t_2;$$

and the annual profit per vessel is simply net revenue minus annual capital cost, i.e.

$$(3) \quad \pi = R - I.$$

Quotas are enforced by season closures. Thus the maximum amount of time that a fishing season can be open is determined by the prevailing catch rate and fleet size as follows.

$$(4) \quad t_i^* = Q_i / (N X_i)$$

The term, $N X_i$, represents the total daily rate of withdrawal from stock i when the fleet is fishing. This rate of catch, divided into the annual quota, determines the length of the open fishing season. Clearly, the more vessels fishing, the shorter the season will be.

FIXED ANNUAL QUOTAS

If there are no natural seasonal variations in fish availability, profit-maximizing vessel operators will fish solely in the most profitable fishery as much of the time as possible. If the fleet size is greater than $(Q_1/X_1 T)$, however, the season for species 1 closes before the vessels have exhausted their fishing capabilities. If the fleet size is greater than $(Q_1/X_1 T)$ but less than $(Q_1/X_1 T) + (Q_2/X_2 T)$, the vessels will be fully utilized in fishing first for species 1 and then for species 2. If the fleet is greater than $(Q_1/X_1 T) + (Q_2/X_2 T)$, both fishing seasons will be closed and the vessels will be idle part of the year. Annual net revenue per vessel is a function of fleet size:

$$(5) \quad R = \begin{cases} r_1 T & \text{if } N \leq Q_1/X_1 T \\ r_1 \frac{Q_1}{X_1 N} + r_2 \left(T - \frac{Q_1}{X_1 N} \right) & \text{if } \frac{Q_1}{X_1 T} < N < \frac{Q_1}{X_1 T} + \frac{Q_2}{X_2 T} \\ r_1 \frac{Q_1}{X_1 N} + r_2 \frac{Q_2}{X_2 N} & \text{if } N > \frac{Q_1}{X_1 T} + \frac{Q_2}{X_2 T} \end{cases}$$

If the two fish stocks are naturally available in two discrete periods of the year (T_1 and T_2), each vessel will seek to fish in both fisheries as much time as possible. Net revenue per vessel is, again, a function of fleet size in three discrete segments. Assuming that stock 1 is the first to be fully exploited,

$$(6) \quad R = \begin{cases} r_1 T_1 + r_2 T_2 & \text{if } N \leq \frac{Q_1}{X_1 T_1}, \quad N \leq \frac{Q_2}{X_2 T_2} \\ r_1 \frac{Q_1}{X_1 N} + r_2 T_2 & \text{if } N > \frac{Q_1}{X_1 T_1}, \quad N \leq \frac{Q_2}{X_2 T_2} \\ r_1 \frac{Q_1}{X_1 N} + r_2 \frac{Q_2}{X_2 N} & \text{if } N > \frac{Q_1}{X_1 T_1}, \quad N > \frac{Q_2}{X_2 T_2} \end{cases}$$

These two equations correspond to curve R in Fig. 1.

Regardless of whether equation (5) or (6) is the appropriate net revenue function, the fleet's total profit is expressed as

$$(7) \quad V = N \cdot (R - I).$$

Assuming that both fisheries yield net revenue ($r_1, r_2 > 0$), the fleet size maximizing V is easily found. If $(r_1T - I)$ is greater than zero for the nonseasonal fishery, then total profit is increased by expanding the fleet up to $N^* = (Q_1/X_1T)$. If the second stock is also profitable, i.e. $(r_2T - I) > 0$, then the fleet should be expanded to $N^{**} = (Q_1/X_1T) + (Q_2/X_2T)$. Any further expansion of the fleet would increase the investment cost but not the net revenue, thus decreasing the profits.

For the case of consecutive natural seasons, if $(r_1T_1 + r_2T_2) > 0$, profits are increased as the fleet expands up to size $N^* = (Q_1/X_1T)$. When the second stock is profitable, i.e. $(r_2T - I) > 0$, the total profit continues to increase until $N^{**} = (Q_2/X_2T)$. Expansion of the fleet beyond the size needed to fully exploit the second stock causes a reduction in profits.

VARIABLE ANNUAL QUOTAS

The numerical example in the text is based upon the algebraic model developed above and the following specific assumptions:

- (1) $P_1 = 10, P_2 = 20$;
- (2) $C_1 = C_2 = 70$;
- (3) $I = 8000$;
- (4) $T = 200$ d;
- (5) $X_{1j} = 10 + .00025 Q_{1j}, X_{1j} = 15 + .000375 Q_{2j}$.

where X_{1j} is the daily catch rate for stock 1 with annual quota level j .

The annual quotas have probability distributions listed in Table 1 of the main text.

Letting f_j represent the probability of quota level j , the expected value of net earnings for a vessel fishing solely stock 1 is

$$(8) \quad E(R) = \sum_j f_j T^* r_{1j},$$

where $T^* = T$ for $N \leq Q_{1j}/X_{1j}T$,

and $T^* = Q_{1j}/X_{1j}$ for $N > Q_{1j}/X_{1j}T$.

This formula was used to compute the expected vessel earnings in columns 2 and 4 of Table 2. Fleet profits, columns 3 and 5 of Table 2, are simply $N \cdot (E(R) - I)$.

In extending the example to multipurpose vessels, it is

TABLE 4. Joint probability distribution for two stock quotas. Correlation coefficient = -0.53 .

Quota 2	Quota 1				
	0	10 000	20 000	30 000	40 000
0	0.00	0.01	0.03	0.04	0.02
20 000	0.01	0.02	0.05	0.12	0.04
40 000	0.03	0.05	0.16	0.05	0.03
60 000	0.04	0.12	0.05	0.02	0.01
80 000	0.02	0.04	0.03	0.01	0.00

assumed that each vessel fishes whichever stock is most profitable until the quota is reached. Once the first quota is reached, the fleet shifts to the less profitable stock. Letting f_{jk} represent the probability that quota level j for stock 1 and quota level k for stock 2 will occur in the same year, the expected net revenue is calculated as follows:

$$(9) \quad E(R) = \sum_{j=1}^5 \sum_{k=1}^5 f_{jk} [T_1^* r_{1j} + T_2^* r_{2k}]$$

where

- (a) $\left. \begin{matrix} T_1^* = T \\ T_2^* = 0 \end{matrix} \right\}$ for $N \leq (Q_{1j}/X_{1j}T)$
- (b) $\left. \begin{matrix} T_1^* = Q_{1j}/X_{1j} \\ T_2^* = (T - T_1^*) \end{matrix} \right\}$ for $(Q_{1j}/X_{1j}T) < N < (Q_{1j}/X_{1j}T) + (Q_{2k}/X_{2k}T)$
- (c) $\left. \begin{matrix} T_1^* = Q_{1j}/X_{1j} \\ T_2^* = Q_{2k}/X_{2k} \end{matrix} \right\}$ for $N > (Q_{1j}/X_{1j}T) + (Q_{2k}/X_{2k}T)$

To permit comparison of the results for different kinds of stock interactions, equation (9) was evaluated over the range of fleet sizes from 4 to 15 vessels and for three different joint probability distributions. The first distribution representing independent stocks follows the rule that $\text{Prob}(X, Y) = \text{Prob}(X) \text{Prob}(Y)$ for X and Y independent. Probabilities for each quota level are the same as those given in Table 1. Competitive stocks are represented by the probability distribution in Table 4, having a negative correlation of -0.53 . The joint probability distribution with positive correlation is created by rotating the probability matrix in Table 4 one-quarter turn.

The Effect of Weather and Other Environmental Variables upon Larval Fish Survival Leading to Recruitment of the Northern Anchovy

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Recent work in the California Current on the effect of weather and other environmental variables upon larval fish survival leading to recruitment of the northern anchovy (Lasker, 1975, 1978) presents us with evidence which clearly shows that in some cases upwelling (Figure 1), while effective in enriching the upper layers of the sea for phytoplankton production, could also be detrimental to larval fish survival because of great dilution of larval fish food organisms and the subsequent replacement of these with diatoms which cannot be fed upon by first-feeding larval anchovy (Figures 2 and 3). Storms also can be detrimental by preventing stratification of potential larval food organisms (Figure 4). The mechanism of dilution keeps the concentration of larval fish food organisms below a threshold needed for supplying the metabolic and growth needs of anchovy larvae.

It has been suggested that the same procedures used for predicting wheat yields in Russia by using climate data bases could be used in fishery predictions. This premise is challenged, for the life history of the anchovy illustrates that the correlation between weather and recruitment cannot be a simple one. Rather, it must take into consideration nuances of the larval life history that are not necessarily consistent from year to year because of biotic and abiotic changes in the environment.

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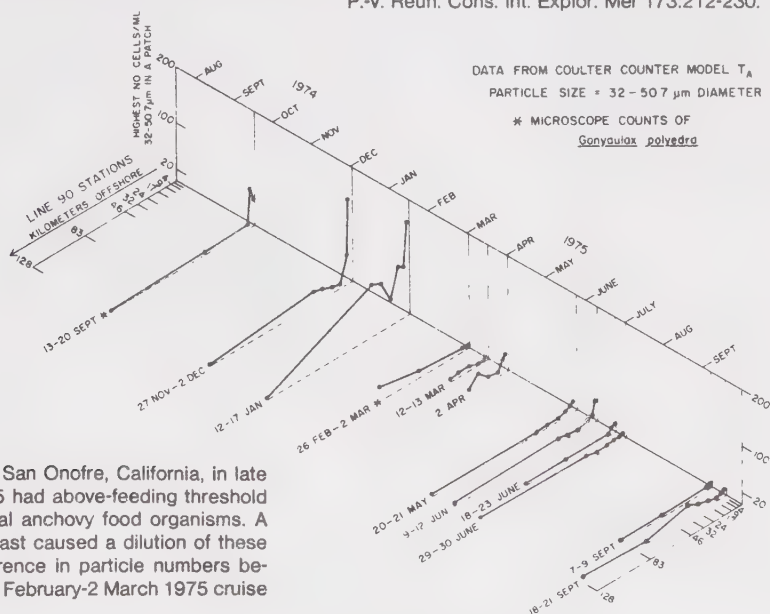


Figure 2. The inshore zone off San Onofre, California, in late 1974 and through January 1975 had above-feeding threshold concentrations of potential larval anchovy food organisms. A massive upwelling along the coast caused a dilution of these food organisms. Note the difference in particle numbers between the 12-17 January and 26 February-2 March 1975 cruise (Lasker, 1978).

A

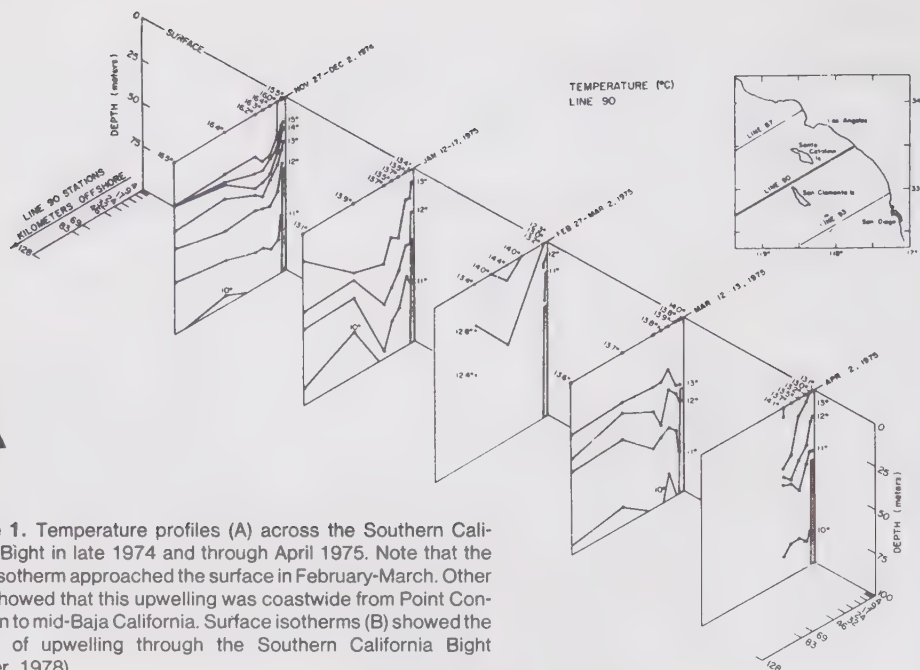
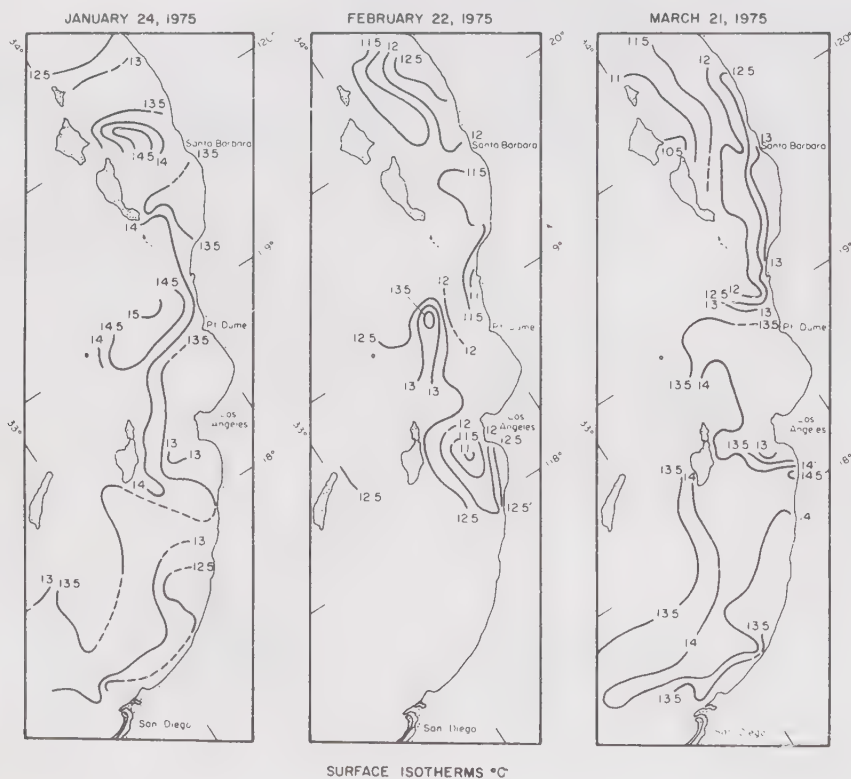


Figure 1. Temperature profiles (A) across the Southern California Bight in late 1974 and through April 1975. Note that the 11°C isotherm approached the surface in February-March. Other data showed that this upwelling was coastwide from Point Conception to mid-Baja California. Surface isotherms (B) showed the extent of upwelling through the Southern California Bight (Lasker, 1978).

B



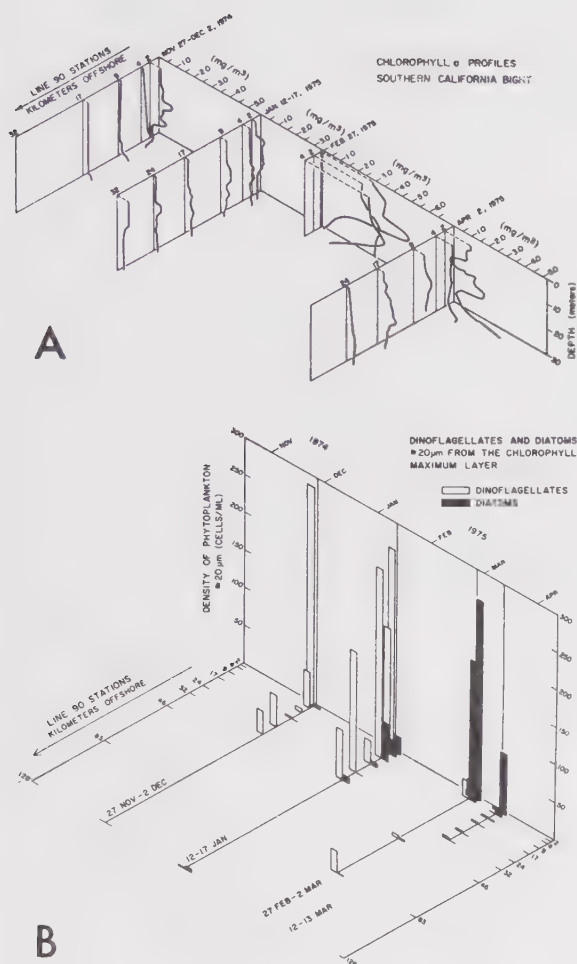


Figure 3. The upwelling shown in Figure 1 resulted in high productivity of diatoms. However, diatoms, unlike dinoflagellates, are not eaten by first-feeding anchovy larvae and do not contribute to their survival. (A) chlorophyll profiles, (B) diatoms replaced dinoflagellates (Lasker, 1978).

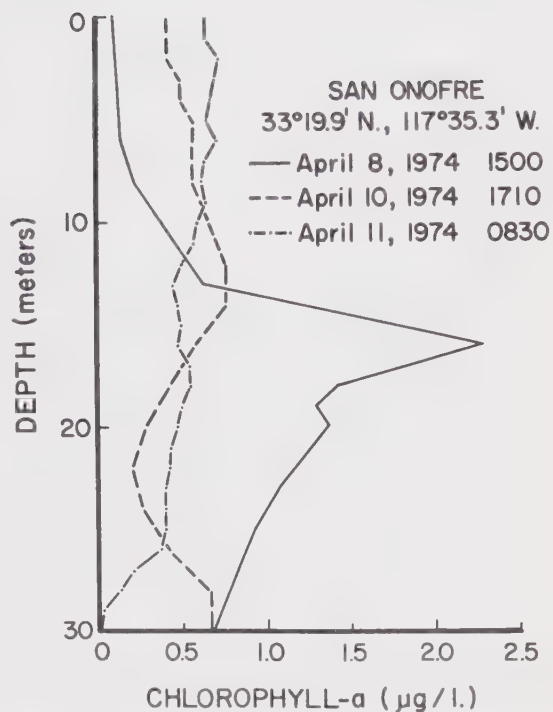


Figure 4. Induced turbulent mixing by storms are also effective in lowering threshold concentrations of larval anchovy food aggregations. In this figure, chlorophyll profiles are shown which were taken the day before and two successive days after a violent wind storm in the Southern California Bight off San Onofre, California. Reduction in chlorophyll indicated the extent of turbulent mixing (Lasker, 1975).

A THEORETICAL EXAMINATION OF SOME ASPECTS OF THE INTERACTION BETWEEN LONGLINE AND SURFACE FISHERIES FOR YELLOWFIN TUNA, *THUNNUS ALBACARES*

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ABSTRACT

This paper explores several aspects of a dual fishery (surface and longline) on yellowfin tuna, *Thunnus albacares*. The work is exploratory in nature and results, though indicative, are not conclusive for any specific fishery. Our results indicate that the yield per recruit is higher for the longline fishery than for surface gear if all fish are available to both gears and higher for the combined gears than for either gear fishing alone. The effect of fishing by one gear on yield to the other gear and the effect of the fishery on stock fecundity is shown to be greater for the often assumed 1:1 sex ratio than for the ratios usually observed. A simulation model was used to examine the interrelations of pattern of movement of fish, pattern of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either only along the coast or throughout the fishing area. The results indicated that either of these patterns of recruitment could allow for increased catch as the surface fleet moved offshore. However, location or pattern of recruitment is shown to be important when measuring natural mortality and for examining the potential of a localized fishery, primarily on younger fish, relative to a fishery exploiting the full range of the stocks or to one taking primarily older fish. Tagging and fecundity studies are suggested for further investigation of the questions examined in this paper.

An unsolved problem common to many of the tuna fisheries of the world is the nature of the interaction between longline and surface (i.e., seining, pole and line, and occasionally trolling and shallow handline) fisheries for the same species. Fisheries for yellowfin tuna, *Thunnus albacares*; albacore, *T. alalunga*; bluefin tuna, *T. thynnus*; southern bluefin tuna, *T. maccoyii*; and bigeye tuna, *T. obesus*, are prosecuted by both types of gear in the Pacific, Atlantic, and Indian Oceans. Although there can be considerable overlap of sizes of fish taken by the two types of gear, in general, longline gear takes larger (older) fish. Exploitation of a tuna stock by the two types of gear presents management with the problems of determining the effect of various combinations of fishing effort by the two gears on both yield per recruit to the two gears and recruitment to the stocks. In order to make these determinations, it is necessary to estimate 1) availability of the stock at each age to each of the two gears [The available portion of the stock is subject to both other mortal-

ity (any mortality not caused by gear of concern) and fishing mortality caused by the gear of concern. The unavailable portion of the stock is subject only to other mortality.], 2) fishing mortality of the available portion of the stock caused by each gear, 3) natural mortality, 4) growth, 5) fecundity, and 6) the relationship between egg production and recruitment.

The aim of this paper is to examine the interactions between longline and surface fisheries for yellowfin tuna and to determine the impact such interactions may have on the assumptions often made in assessment of yellowfin tuna fisheries and thus on the assessment calculations themselves. The paper is divided into three major sections. The first section examines the relationship between availability of the stock(s) of yellowfin tuna to surface and longline fishing and yield per recruit to the two gears. This is an important, and to our knowledge unexamined, aspect of all tuna fisheries exploited by both types of gear; the subsequent sections examine two aspects of the biology of tuna that can affect the catch by each type of gear. The second section examines the effect of age specific sex ratios of yellowfin tuna on yield per recruit to the two types of gear and on egg production. The third section examines the effect of

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random migration or dispersal and location of recruitment of yellowfin tuna on estimates of mortality and yield per recruit to each gear. We have restricted our analysis to yellowfin tuna but believe that the concepts that we develop apply to the other species as well.

MATERIALS AND METHODS

While stocks of yellowfin tuna are subjects of important fisheries in all tropical oceans, information on vital parameters is sketchy and nonuniform. For example, tagging information available in the Pacific is lacking for the Atlantic stocks. On the other hand, regulation of the Pacific fishery makes interpretation of the catch information more difficult. Hence it is necessary to pick and choose from the available information that which is most relevant to the problems at hand. Although the parameters are likely to differ for fish from different oceans, if not fish from different areas of the same ocean, few studies have conclusively demonstrated that such differences exist. In addition, several (e.g., Lenarz et al. 1974) have found that conclusions from studies such as described in this paper are often insensitive to the likely range of values of parameters such as natural mortality, fishing mortality, and growth. In the first and second sections, we have used data primarily from the eastern Atlantic because historically catches have been more equally shared by longline and surface fisheries than in the eastern Pacific; in the third section we have modelled the eastern Pacific since information on migration patterns is more extensive. In both instances, the results are intended to be general rather than specific. Data extracted from one area and used in another is thought to be the best available and the question of real differences is left for further investigation.

With a noted exception, the growth equation $L = 194.8 \times (1 - e^{-0.42(t-0.67)})$ estimated by Le Guen and Sakagawa (1973) and length-weight equation $W = 0.000214L^{2.9736}$ estimated by Lenarz (1974) are used for yellowfin tuna where L is fork length in centimeters, t is age in years, and W is weight in kilograms. Unless otherwise stated, we assumed that the annual instantaneous coefficient of natural mortality (M) is 0.8 (Hennemuth 1961). We estimated age-specific fecundity from two indices derived by Hayasi et al. (1972) (Table 1). Their index I was obtained from longline data and their index II was obtained from surface data. The

TABLE 1.—Indices of fecundity of yellowfin tuna as interpolated from Hayasi et al. (1972), for fish caught in the Pacific calculated by multiplying average ova counts by percentage of mature female fish for each age and then dividing each product by the product calculated for age 3 fish.

Midpoint of size interval (cm)	Fecundity index I	Fecundity index II
80	0.04	0.07
85	0.04	0.14
90	0.05	0.21
95	0.08	0.27
100	0.15	0.36
105	0.23	0.42
110	0.33	0.51
115	0.42	0.61
120	0.55	0.70
125	0.70	0.81
130	0.88	0.92
135	1.12	1.04
140	1.40	1.15
145	1.80	1.26
150	2.30	1.37
155	2.77	1.50
160	3.20	1.62
165	3.57	1.76
170	4.05	1.91
175	4.42	2.06
180	4.82	2.23
	5.01	2.43

fecundity indices were calculated by Hayasi et al. (1972) for fish caught in the Pacific by multiplying mean ova counts by percentage of mature female fish for each age and then dividing each product by the product calculated for age 3 fish. For much of our work, we used estimates of the 1967-71 average size (age) composition of the Atlantic yellowfin tuna fishery made by Lenarz et al. (1974) (Table 2). Use of length-age key assumes that length and age are equivalent. Sex composition shown in Table 2 is based on data from the Pacific.

Estimates of the size- (age-) specific instantaneous coefficient of fishing mortality (F_t) on an annual basis were made using the Gulland (1965) and Murphy (1965) method. The computer program COHORT, written by W. W. Fox, Jr., of the Southwest Fisheries Center, was used to obtain estimates of F_t for each 5-cm size interval, beginning at 32.5 cm. The estimation procedure was initiated with a trial value of F_t for the largest size interval (Input F).

Estimates of F_t were obtained from the average 1967-71 catch composition data (Table 2) as was done by Lenarz et al. (1974). When feasible it is more desirable to estimate F_t from individual cohorts. This was not done because of the small number of years in the data series and belief that estimates from the average composition would adequately reflect conditions of the fishery. In a latter study, Fonteneau and Lenarz (1974) estimated F_t for individual cohorts from a longer time

TABLE 2.—Composite catch in numbers of yellowfin tuna by gear, sex, and size. Length composition by gear is based on data from Lenarz et al. (1974) on the Atlantic fishery. Sex composition is based on data from the Pacific (Murphy and Shomura 1972).

Age at beginning of interval (yr)	Midpoint of size interval (cm)	Male			Female		
		Surface	Longline	Total	Surface	Longline	Total
1.0579	35	1,179	0	1,179	1,179	0	1,179
1.1325	40	14,528	0	14,528	14,528	0	14,528
1.2039	45	61,563	0	61,563	61,563	0	61,563
1.2888	50	186,611	4	186,615	186,611	4	186,615
1.3710	55	237,622	11	237,633	237,622	11	237,633
1.4562	60	210,711	226	210,937	210,711	226	210,937
1.5445	65	121,824	324	122,148	121,824	324	122,148
1.6363	70	137,389	1,076	138,465	137,389	1,076	138,465
1.7317	75	102,046	2,718	104,764	102,046	2,718	104,764
1.8310	80	90,710	2,847	93,557	90,710	3,847	93,557
1.9348	85	67,060	6,013	73,073	67,060	6,013	73,073
2.0432	90	52,541	6,525	59,066	52,541	6,525	59,066
2.1568	95	51,366	5,833	57,199	51,366	5,833	57,199
2.2761	100	56,714	7,537	64,251	56,714	7,537	64,251
2.4017	105	52,752	17,036	69,788	52,752	17,036	69,788
2.5343	110	51,497	20,105	71,602	51,497	20,105	71,602
2.6748	115	35,981	22,017	57,998	35,981	22,017	57,998
2.8240	120	26,167	21,430	47,597	26,167	21,480	47,597
2.9832	125	30,779	28,679	59,458	30,779	28,679	59,458
3.1538	130	26,001	29,272	55,273	26,001	29,272	55,273
3.3376	135	21,975	22,345	44,320	21,975	22,345	44,320
3.5368	140	16,749	26,035	42,784	16,749	26,035	42,784
3.7542	145	26,919	38,782	65,701	11,661	16,800	28,461
3.9935	150	31,942	36,099	68,041	8,450	9,549	17,999
4.2595	155	24,727	33,933	58,665	3,767	5,170	8,937
4.5590	160	18,701	22,644	41,345	1,524	1,845	3,369
4.9017	165	14,497	13,140	27,637	573	519	1,092
5.3021	170	5,621	6,162	11,783	94	103	197
5.7838	175	3,703	240	3,943	21	1	22
6.3883	180	1,836	55	1,891	3	0	3
Total		1,781,711	371,093	2,152,804	1,679,858	254,020	1,933,878

span and obtained results similar to Lenarz et al. (1974).

The computer program MGEAR, written by W. H. Lenarz, was used to obtain estimates of yield per recruit using the Ricker (1958) yield equation. A description and listing of MGEAR is available from its author. The program was slightly modified to calculate indices of egg production using the following equation

$$E_{t_1, t_2} = 0.5 (t_2 - t_1) N_{t_1} (FI_{t_1} + FI_{t_2} e^{-(F_{t_1} + M_{t_1})(t_2 - t_1)})$$

where E_{t_1, t_2} = index of egg production between age t_1 and t_2 ,

FI_{t_1} = index of fecundity for age t_1 ,

N_{t_1} = number of females in population of age t_1 ,

F_{t_1} = coefficient of instantaneous fishing mortality between age t_1 and age t_2 , and

M_{t_1} = coefficient of instantaneous natural mortality between age t_1 and age t_2 .

For this equation it is assumed that the estimates of FI are proportional to egg production per

female, which is assumed to be continuous, and that the rate of egg production is linear over the interval (t_1, t_2) .

A computer program MIGR was written by J. R. Zweifel to perform the calculations used for the third section of this paper. Since new methodology is developed, a description of the calculations will be given in that section.

AVAILABILITY OF THE STOCK(S) OF ATLANTIC YELLOWFIN TUNA TO SURFACE AND LONGLINE GEAR

In previous works on yield per recruit, yellowfin tuna of all ages in either the entire Atlantic (e.g., Hayasi and Kikawa 1970; Wise 1972; Hayasi et al. 1972; Lenarz et al. 1974), or in the eastern Atlantic (e.g., Fonteneau and Lenarz 1974) were assumed to be equally available to both longline and surface gear. However, since the surface fishery for yellowfin tuna occurs very close to the west African coast (Fox and Lenarz 1973) while the longline fishery for yellowfin tuna is distributed throughout the tropical Atlantic, it seems possible that the longline fishery is exploiting some fish that are not available to the surface fishery. It is

also possible that some stock(s) which are available to surface fishing are never available to the longline fishery. Since significant tagging efforts have begun only recently in the Atlantic and the results of these studies have not been published, data are not available to evaluate the availability of yellowfin tuna to both gears.

However, there is evidence from the Pacific that yellowfin tuna are not equally available to longline and surface gears. With the permission of W. H. Bayliff of the Inter-American Tropical Tuna Commission (IATTC), we examined yellowfin tuna tag return data from the eastern Pacific during 1963-66 in an attempt to evaluate the availability of fish to both gears in that area. We tabulated the number of tag returns for fish larger than 100 cm at return by 10-cm size groups (Table 3). All of the fish had been at liberty for at least 10 mo. Although all of the tagged fish were measured when released, not all were measured when recovered. Bayliff recommended the relationship

$$L = 167 (1 - e^{-0.61(t-0.833)})$$

estimated by Davidoff (1963) for growth of yellowfin tuna in the eastern Pacific as the best equation to estimate the size of unmeasured fish. All of the returns were surface-caught fish, even though longliners captured a considerable number of yellowfin tuna in the eastern Pacific (east of long. 130°W) (Kume and Joseph 1969). In fact for many of the 10-cm size groups, the longliners caught more yellowfin tuna than the surface gear operators (Table 4).

TABLE 3.—Number of returns of tagged yellowfin tuna from the eastern Pacific Ocean by size interval and year (W. H. Bayliff, pers. commun.).

Size interval (cm)	1963	1964	1965	1966
101-110	2	16	3	3
111-120	1	7	1	1
121-130	2	0	2	0
131-140	0	0	0	1
141-150	0	0	0	0
151-160	0	0	1	0

Again at the suggestion of Bayliff, we estimated the expected return of tags from longline-caught fish when all fish are equally available to both gears. Assuming tag recoveries were independent of each other, recovered tags were reported at the same rate by both components of the fishery, and tagged fish were equally available to both gears: then the expected returns of tagged fish of size i by gear j in year k is given by

$$E(R_{ijk}) = R_{i \cdot k} N_{ijk} / N_{i \cdot k} \quad (1)$$

$$i = \begin{cases} 1, & \text{when size is between 101 and 110 cm} \\ \vdots & \\ 6, & \text{when size is between 151 and 160} \end{cases}$$

$$j = \begin{cases} 1, & \text{when fish are caught by surface gear} \\ 2, & \text{when fish are caught by longline gear} \end{cases}$$

$$k = \begin{cases} 1, & \text{when fish are caught in 1963} \\ 2, & \text{when fish are caught in 1964} \\ 3, & \text{when fish are caught in 1965} \\ 4, & \text{when fish are caught in 1966} \end{cases}$$

where R_{ijk} = number of returns and
 N_{ijk} = number of fish caught.

A dot in the position of a subscript signifies summation of the variable over the subscript, e.g., $X_{i \cdot k}$
 $= \sum_{j=1}^2 X_{ijk}$.

Forty fish were returned by the surface gear during 1963-66 (Table 3). Using the statistics of Tables 3 and 4 and the three assumptions, a return of 5.4 of these tags would have been expected from the longline fishery and 34.6 from the surface fishery. The chi-square value, corrected for discontinuity, for the observed and expected returns (Equation 1) is 5.13, with probability slightly less than 0.025. The power of the test of the hypothesis of independence, equal reporting rate, and equal availability was reduced because we combined the year and size strata to avoid

TABLE 4.—Catch of yellowfin tuna from the eastern Pacific Ocean (east of long. 130°W) in hundreds of fish by size and gear (Kume and Joseph 1969).

Size interval (cm)	1963		1964		1965		1966	
	Surface gear	Longline gear	Surface gear	Longline gear	Surface gear	Longline gear	Surface gear	Longline gear
101-110	653	336	4,082	173	3,386	30	2,926	54
111-120	473	455	2,245	465	2,211	93	2,044	116
121-130	508	390	720	1,078	1,895	444	1,312	304
131-140	237	751	448	804	905	758	718	515
141-150	240	541	320	469	498	466	536	575
151-160	212	144	102	104	194	205	204	200

strata with low expected values. The probability under Equation (1) of a returned tag being from a surface-caught fish (P_{i1k}) is

$$P_{i1k} = N_{i1k}/N_{i \cdot k} \quad (2)$$

The exact probability of all returns during the 1963-66 period being from surface-caught fish, given the distribution of returns among year and size categories, is

$$P_{.1.} = \prod_{i=1}^6 \prod_{k=1}^4 (P_{i1k})^{R_{i \cdot k}} \quad (3)$$

Our estimate of $P_{.1.}$ is 0.00152, which is very low and indicates that Equation (1) does not hold. Thus we may conclude that 1) tag returns are not independent (e.g., fish that were captured from a school and tagged may remain in the same school until recaptured), and/or 2) longline recoveries are reported at lower rates than surface recoveries, and/or 3) the fish were not equally available to both gears. Since all fish were at liberty for more than 10 mo before being recovered, the assumption of tag returns being independent seems likely to be valid. The independence of tag returns would seem to be a desirable subject for further research since the assumption is so often made in analyses of tag returns. A considerable number of southern bluefin tuna have been recovered and returned by longliners (Shingu 1970), indicating longline fishermen do cooperate in tagging programs. During the period of the study, the surface fishery was only beginning to move offshore (Calkins and Chatwin 1971), while the longline fishery was distributed throughout the area (Kume and Joseph 1969). Also, the fish that were released were caught by surface gear, tagged, and released in nearshore areas. Thus, tagged fish were probably more representative of fish exploited by the surface fishery than those that were exploited by the longline fishery, if two groups of fish existed. Thus it seems plausible that the tagged fish were not equally available to longline and surface gears.

This is further evidence of unequal availability of yellowfin tuna to the two gears in the Pacific. Previously, Hisada (1973) showed that yellowfin tuna caught near the surface using handlines were of the same size as those caught by longliners at the same time and in the same area of the western Pacific. However, the surface-caught fish tended to be more sexually mature except in areas in which the 26°C isotherm occurred at depths

fished by longliners. He attributed this phenomenon to a preference for warmer waters by sexually mature fish and noted that larvae of yellowfin tuna tend to be found at water temperatures exceeding 26°C. Thus, some yellowfin tuna evidently behave in a fashion that makes them available to surface fishing but not to longline fishing. Further evidence along these lines is provided by Shingu and Tomlinson (Patrick K. Tomlinson, Inter-American Tropical Tuna Commission, La Jolla, Calif. Pers. commun., 1974) who found that the length-weight relationship estimated by Lenarz (1974) for surface-caught yellowfin tuna in the Atlantic was more representative of the longline catch in the eastern Pacific than was the relationship estimated by Chatwin (1959) for surface-caught yellowfin tuna in the eastern Pacific.

With the above in mind, we considered three hypothetical stock structures for the Atlantic yellowfin tuna fishery: 1) the same stock(s) are equally available to both gears, 2) half of the catch of the longline fishery comes from stock(s) not available to the surface fishery, and 3) the entire catch of the longline fishery comes from stock(s) not available to the surface fishery. The effects of the three hypotheses on estimates of fishing mortality and yield per recruit to the gear were examined.

Using the data in Table 2, we estimated the vector F of size-specific instantaneous mortality rates F_i under the three hypotheses which are identified by the proportion ϕ of the longline catch which comes from the stocks exploited by the surface fishery as $\phi = 1.0, 0.5$, and 0.0 respectively. For $\phi = 1.0$, all of the data in Table 2 was used to estimate the F vector. For $\phi = 0.5$, the surface catch plus 50% of the longline catch was used and for $\phi = 0.0$ only the surface catch was used for estimating F . When $\phi = 0$, an additional F vector was estimated for a longline fishery operating without the presence of a surface fishery by using only the longline catch. The F vectors were then used to calculate yield per recruit to the two gears. Estimation of a vector of size-specific F requires an estimate of natural mortality and size-specific F for one size category. In all instances, we chose to use an estimate of size-specific F for the fish >177.5 cm. This estimate will be referred to as Input F . The final value of size-specific F was set at 0.2 following Lenarz et al. (1974). The estimates (Figure 1) indicate that values of F for large fish are directly related to the portion of the longline catch that comes from the stock(s) exploited by the

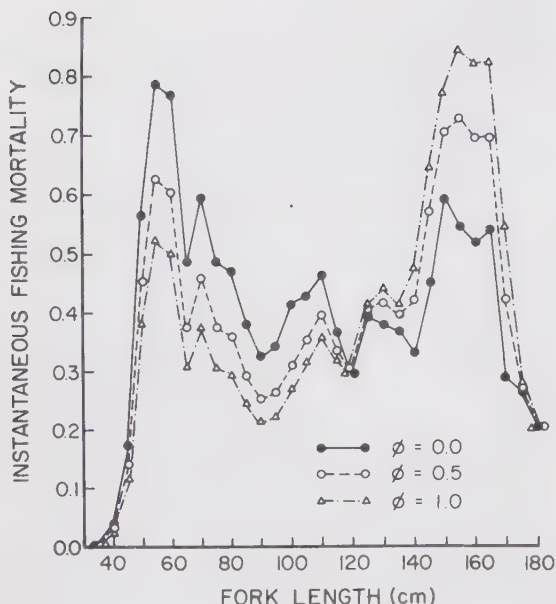


FIGURE 1.—Estimates of size-specific fishing mortality of Atlantic yellowfin tuna as a function of proportion of catch (ϕ) by longline fishery that comes from stock(s) exploited by surface fishery.

surface fishery. The relative values of yield per recruit within a hypothesis are not significantly affected by the portion of the longline catch that comes from the stock(s) exploited by the surface fishery (Figure 2). Therefore, the three hypothetical stock structures do not seem to have much bearing on decisions concerning minimum size regulations.

Estimates of yield per recruit were also plotted as functions of fishing effort (mortality), size at recruitment, and portion of longline catch that comes from stock(s) exploited by the surface fishery. Again the relative values of the results are not significantly influenced by the stock structure (Figure 3a, b). We note that Figure 3 is in agreement with the conclusion of Fox and Lenarz (1974), "... that the Atlantic yellowfin fishery is approaching or has obtained a plateau where substantially increased sustainable average yield of yellowfin tuna will not be obtained by increasing fishing effort without some concomitant change in the constitution of the fishery. ..." They used the production model approach under the alternative assumptions that either the longline or surface gear exploits the same or separate stock(s).

The effect of the surface fishery on the longline fishery was examined by estimating yield per re-

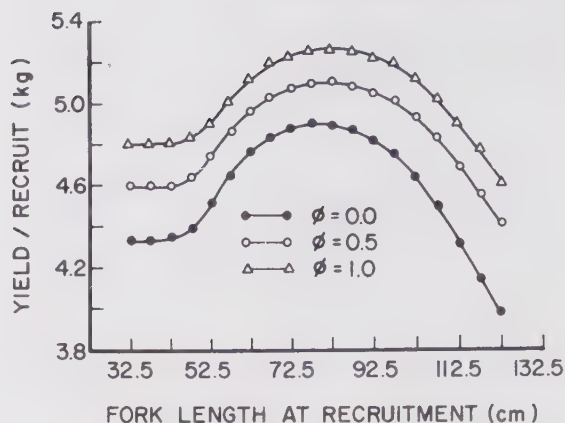


FIGURE 2.—Yield per recruit (kilograms) of Atlantic yellowfin to surface and longline gear as a function of size at recruitment and proportion of catch (ϕ) by the longline fishery that comes from stock(s) exploited by surface fishery. The vector of fishing mortality is equal to the value at the time of study.

cruit to the longline fishery in the presence and in the absence of a surface fishery (Figure 4). The results suggest that if the two gears exploit the same stock(s), the surface fishery reduces the potential yield per recruit to the longline fishery by about twofold at the position of the fishery during the study period (i.e., multiplier of effort = 1) and about fivefold for a threefold increase in effort. The same procedure was used to examine the effect of the longline fishery on the surface fishery (Figure 5). The results indicate that at the level of fishing effort at the time of study, the yield per recruit to the surface fishery would be increased by 25% if the longline fishery ceased.

Although the presence of each fishery reduces the yield per recruit of the other, the yield per

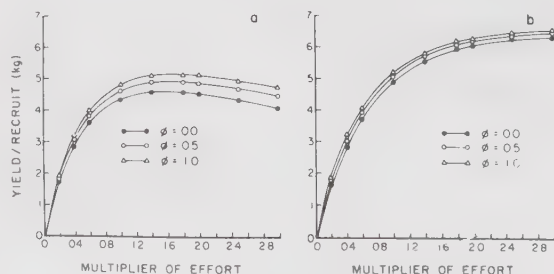


FIGURE 3.—Yield per recruit of Atlantic yellowfin tuna as a function of fishing effort and proportion of catch (ϕ) by longline fishery that comes from stock(s) exploited by surface fishery: (a) size at recruitment is 32.5 cm, (b) size at recruitment is 77 cm.

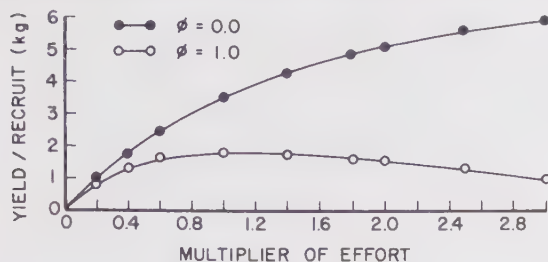


FIGURE 4.—Estimates of yield per recruit of Atlantic yellowfin tuna to the longline fishery as a function of effort and presence ($\phi = 1.0$) or absence ($\phi = 0.0$) of a surface fishery.

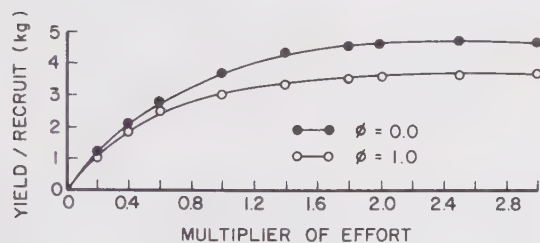


FIGURE 5.—Estimates of yield per recruit of Atlantic yellowfin tuna to the surface fishery as a function of effort and presence ($\phi = 1.0$) or absence ($\phi = 0.0$) of longline fishery.

recruit of the combined fisheries is higher than the yield per recruit of either fishery alone. The results suggest that if a catch quota system is imposed on the Atlantic yellowfin tuna fishery, all components should be included unless it is shown that different stock(s) are being exploited by the gear.

The above results (Figures 4, 5) suggest that a stock of yellowfin tuna will produce a potentially higher yield per recruit to a longline fishery than to a surface fishery, if the fish are equally available to the two gears. However, until the question of availability is settled, it is not possible to predict the potential production to the two gears. We point out here that gear-specific availability is not well known for any tuna fishery and would be difficult to determine. Thus, we are faced with the prospect of probably being forced to determine empirically the production potential for each gear in each fishery. After a fishery is established, an analysis of the type conducted on the Atlantic yellowfin tuna fishery could be used to examine the effects of availability to the two gear types, and a tagging study could be designed to provide the required answers.

EFFECTS OF AGE-SPECIFIC SEX RATIOS OF ATLANTIC YELLOWFIN TUNA ON YIELD PER RECRUIT TO THE TWO TYPES OF GEAR AND STOCK FECUNDITY

While a number of authors have noted that the ratio of females to males appears to be less than 1:1 for catches of larger tunas, none to our knowledge has incorporated these observations into calculations of yield per recruit or stock fecundity. Beardsley (1971) reported that the ratio of female to male Atlantic longline-caught albacore was 233:365 during the December 1969-September 1970 period. Males increasingly dominated at sizes >100 cm. Females slightly outnumbered males between 92 and 100 cm. One explanation for the catch curves estimated by Beardsley is a 1:1 sex ratio at small sizes, a slightly slower growth for females for fish >90 cm, and beyond 100 cm, either a higher rate of natural mortality for females or a change in behavior that makes females less available than males to longline fishing. Other explanations exist, e.g., a combination of low sex ratio and slow growth of females throughout their life. Sakamoto (1969) noted for Atlantic bigeye tuna, "... males predominated in areas of higher water temperature. Proportion of females increase as the water temperature gets lower." His data indicate that as size increases the proportion of females decreases and females may grow slower than males in waters between lat. 30° to 50° N, but not in equatorial waters. Data presented by Kikawa (1964) indicate that southern bluefin tuna >150 cm are predominantly males, while females often outnumber males at smaller sizes. Thus, female southern bluefin tuna may grow more slowly than males.

Since there is considerable evidence for age-specific changes in the sex ratio of tunas, we believe that the effects of such changes on estimates of yield per recruit to each gear type and fecundity should be investigated. We have assumed sex ratios to be the same as with Pacific yellowfin tuna because no extensive studies of age-specific sex ratios for Atlantic yellowfin tuna have been published. We used results from a study by Murphy and Shomura (1972), who found that beyond 140 cm male yellowfin tuna greatly outnumbered females (Figure 6). The data in Figure 6 do not show a large excess of females in any size interval and thus no evidence of sex-specific growth is exhibited. Using their data and the age-length

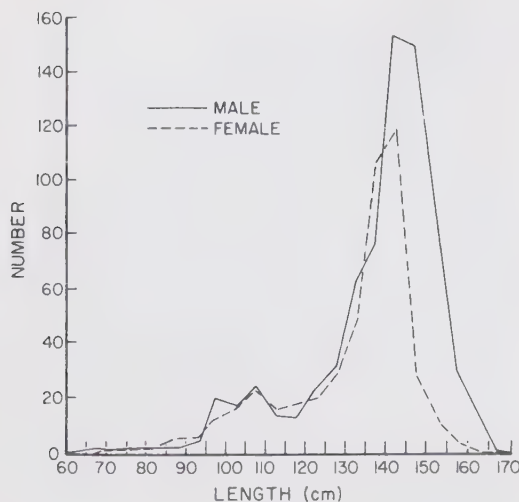


FIGURE 6.—Length distribution by sex of longline-caught yellowfin tuna in the central Pacific Ocean (Murphy and Shomura 1972).

relationship of LeGuen and Sakagawa (1973), we estimated that beyond 140 cm

$$\ln R = 6.74 - 1.96t \quad (4)$$

where R = ratio of females to males
 t = age in years.

One interpretation of the above result (assuming that males have a coefficient of instantaneous natural mortality of 0.8 on an annual basis as do all fish <145 cm) is that female yellowfin tuna >140 cm have a coefficient of apparent natural mortality of 2.76. Assuming that the results of Murphy and Shomura apply to the Atlantic and that all yellowfin tuna are equally available to both gears, we separated the catch of yellowfin tuna into males and females using Equation (4) and Table 2, and estimated F for the males using Input F values of 0.2 and 0.8 for fish >177.5 cm (Lenarz et al. 1974). An alternative method would be to use the same Input F for the three hypotheses at the smallest size interval. This was attempted and resulted in either estimates of F_i which, based on the results of other studies, appeared to be too low under the 1:1 hypothesis or too high under the other hypotheses. The estimates of size-specific F are similar except for very large yellowfin tuna (Figure 7). Since the deviations in sex ratio from 1:1 occurs only at large sizes, we used both sets of estimates of F .

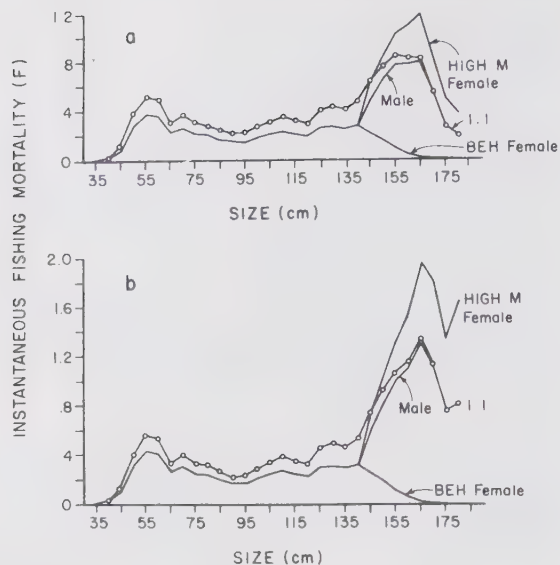


FIGURE 7.—Estimates of size and sex specific coefficient of instantaneous fishing mortality on annual basis (F) for Atlantic yellowfin tuna for 1:1, BEH and HIGH M hypotheses (see text): (a) low Input F , (b) high Input F .

For females, three hypotheses were examined for estimating F : 1) the observed differences in sex ratios are artifacts, and consequently females have the same values of F and M as males (denoted 1:1); 2) females >140 cm have a higher natural mortality rate than males but are exploited at the same rate as males for all sizes (denoted as HIGH M); and 3) females have the same natural mortality rate as males but become less subject to fishing mortality beyond 140 cm (denoted as BEH for behavior changes). Under the BEH hypothesis, F_i for females >140 cm is equal to the ratio of the catch of females to the catch of males times F_i estimated for males. The alternative hypotheses considerably affected the estimates of size-specific F (Figure 7).

In the following analyses, we found that the BEH and HIGH M hypotheses produce similar results. To save space, we refer to only the one hypothesis that produced results which showed the greatest difference from the 1:1 hypothesis. Also, when not specifically indicated, size of recruitment and effort are assumed to be those at the time of the study, i.e., 1967-71 where the multiplier of effort is equal to unity.

Estimates of yield per recruit as a function of fishing effort are shown in Figure 8. The choice of Input F has little effect on the relative values of

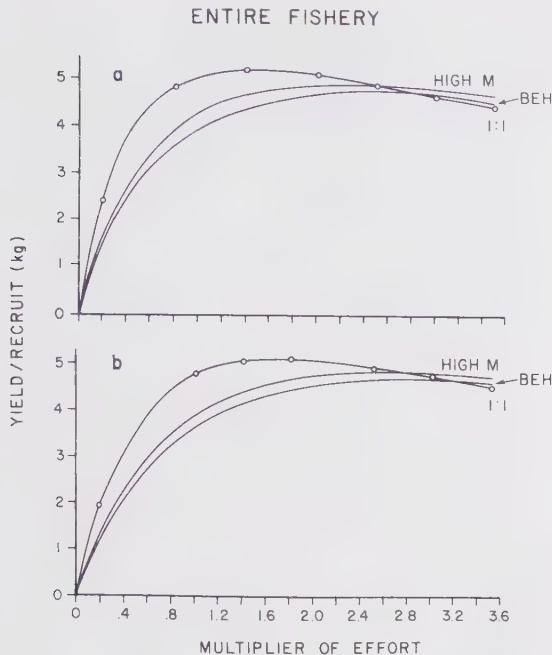


FIGURE 8.—Estimates of yield per recruit of Atlantic yellowfin tuna at size of recruitment at time of the study as a function of fishing effort and sex hypothesis: (a) high Input F , (b) low Input F .

yield per recruit. Yield per recruit is closer to the maximum under high Input F than low Input F . The curves are considerably more dome-shaped when a 1:1 sex ratio is assumed than under the other two hypotheses. Under high Input F and the 1:1 hypothesis only a 3% increase in yield per recruit could be obtained by increasing fishing effort. Under the BEH hypothesis, a 20% increase in yield per recruit could be obtained by doubling the effort.

Estimates of yield per recruit as a function of size at recruitment are shown in Figure 9. Again the choice of Input F has little effect on the relative values of yield per recruit. A slightly greater dependence of yield per recruit on minimum size is obtained when the high Input F is used. Under high Input F , and the 1:1 hypothesis a 10% increase in yield per recruit could be achieved by increasing size at recruitment. Under the BEH hypothesis, only a 5% increase would occur. Eumetric fishing occurs when size at recruitment is raised from the current 32.5 to 82.5 cm under the 1:1 hypothesis and 72.5 cm under the BEH hypothesis.

Estimates of yield per recruit as a function of fishing effort were also calculated for each gear

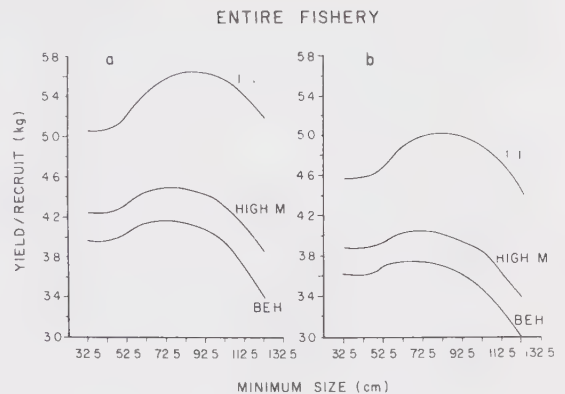


FIGURE 9.—Estimates of yield per recruit of Atlantic yellowfin tuna at level of fishing effort at the time of the study for 1:1, BEH and HIGH M hypotheses as a function of size at recruitment: (a) high Input F , (b) low Input F .

(Figure 10). The results show that the curves are more dome-shaped for the longline fishery than for the surface fishery under all three hypotheses. Furthermore, the longline fishery is more sensitive to fishing effort under the 1:1 hypothesis than under the other two. The curves for the surface fishery are dome shaped under the 1:1 hypothesis, but appear to approach an asymptote under the other two.

We also estimated yield per recruit for each gear when the other gear is not exploiting the stock (Figure 11). A comparison of Figures 10 and 11 reveals that yield per recruit to the longline fishery would increase by about 115% if surface fishing were eliminated under high Input F and the 1:1 hypothesis and 76% under high Input F and the BEH hypothesis. Yield per recruit to the surface fishery would increase by about 30% if the longline fishery were eliminated under high Input F and the 1:1 hypothesis and 22% under the BEH hypothesis. Thus, the nature of age-specific sex ratio has a greater effect on that of the longline fishery than on the relative success of the surface fishery. The curves for a longline fishery in the presence of a surface fishery are dome-shaped (Figure 10), while the curves in the absence of a surface fishery are not (Figure 11). This again points out the importance of not treating the two fisheries as separate entities unless it is shown that they exploit separate stocks.

Stock fecundity (egg production per recruit) relative to an unfished stock was estimated as a function of fishing effort. Stock fecundity was considerably affected by the choice of fecundity index

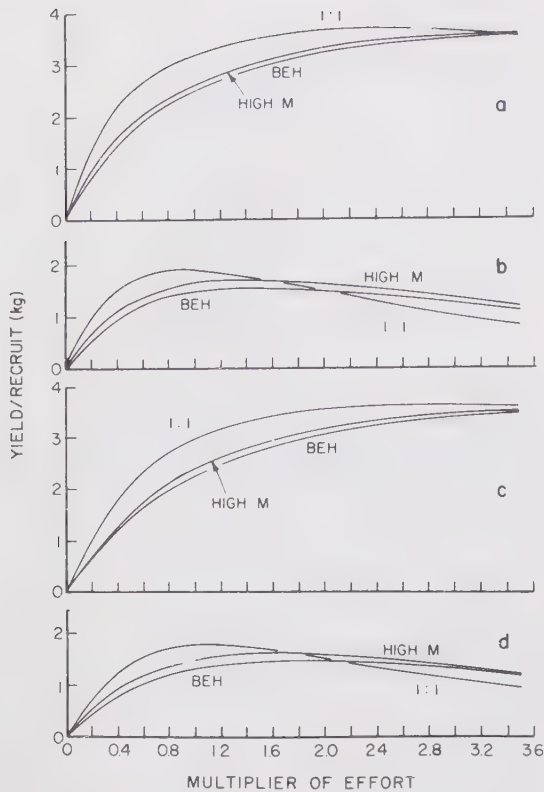


FIGURE 10.—Estimates of yield per recruit of Atlantic yellowfin tuna when both gear fish at size of recruitment at the time of the study as a function of sex ratio hypothesis, fishing effort, and gear: (a) surface gear with high Input F , (b) longline gear with high Input F , (c) surface gear with low Input F , and (d) longline gear with low Input F .

and sex ratio hypothesis but only slightly affected by the choice of Input F (Figure 12). At the level of fishing effort at the time of the study under high Input F and 1:1 hypotheses, the relative fecundity is 0.28 when the fecundity index I is used and 0.39 when fecundity index II is used. Under the HIGH M hypothesis, relative fecundity is 0.55 when fecundity index I is used and 0.61 when fecundity index II is used. Thus, at the level of fishing effort at the time of the study, the choice of fecundity has a 10 to 30% effect on estimates of relative fecundity, while the choice of sex ratio hypothesis has a 30 to 50% effect. The two choices, fecundity index and sex ratio hypothesis, also have considerable effect on relative fecundity when plotted as a function of size at recruitment (Figure 13).

The relationship between stock fecundity and recruitment has not been demonstrated for any tuna. As shown above, one of the difficulties in

demonstrating such a relationship is obtaining a reasonably accurate estimate of stock fecundity. Even if stock fecundity could be accurately determined, the recruitment process is likely to be so complex that much more research would be required before a reliable predictor of recruitment could be developed.

It is interesting to note that similar estimates of yield per recruit and relative fecundity are obtained under the HIGH M and BEH hypotheses. Thus it appears that research should be directed toward determining whether or not the 1:1 hypothesis or one of the other two are valid rather than distinguishing between the HIGH M and BEH hypotheses. This research should be a fairly simple matter. The choice of fecundity index is also of significance for estimating relative fecundity. The difference between the two indices is caused mainly by different maturity schedules (Hayasi et al. 1972). The surface-caught fish appeared to mature at an earlier age than longline-caught fish, and could be an artifact related to the phenomenon noted by Hisada (1973); i.e., mature fish tend to prefer warm water. It should also be a fairly simple matter to determine the cause of the difference between the two indices.

SIMULATION MODEL OF PATTERNS OF DISPERSAL AND RECRUITMENT OF YELLOWFIN TUNA

Factors that could cause groups of tuna to not be available to all components of a fishery include nonrandom movements, random movements but nonrandom distribution of fishing gear or effort, and recruitment that is nonrandom in a geographical sense.

Extensive tagging experiments have not produced any clear-cut evidence of a definite migration pattern for yellowfin tuna in the eastern Pacific. Bayliff and Rothschild (1974) recently found evidence for both random dispersal and directed movements. They were not able to remove the effects on their data of lack of fishing effort in some time-area strata and of the coastal boundary. The evidence for directed movements indicated that such movements were generally parallel to the coast, suggesting that the presence of the coast influenced their results. Fink and Bayliff (1970), in a synthesis of extensive tagging data, proposed that recruitment to the nearshore surface fishery is not random in a geographical sense, but tends to take place off Mexico and in the Panama Bight.

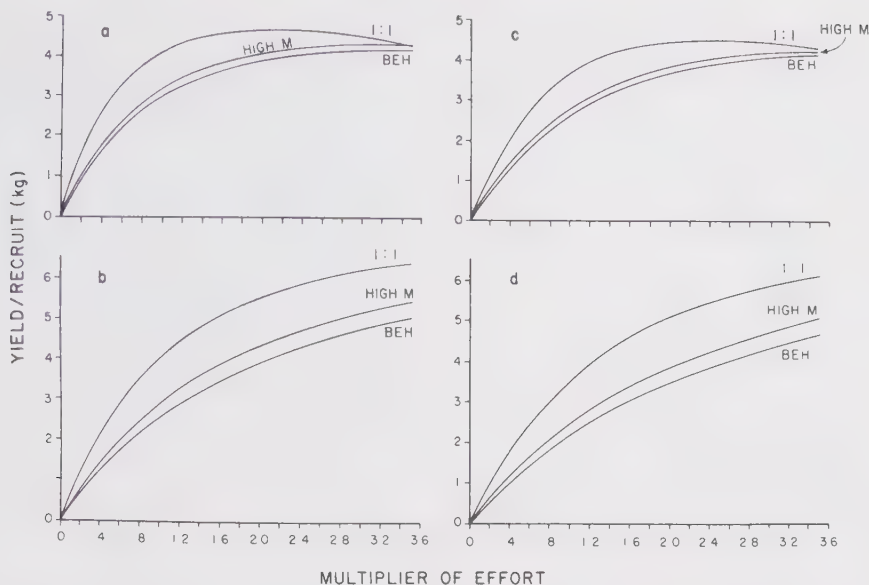


FIGURE 11.—Estimates of yield per recruit at size at recruitment at the time of the study as a function of fishing effort, sex ratio hypothesis, and fishing gear when only one gear is fishing: (a) high Input F and surface gear, (b) high Input F and longline gear, (c) low Input F and surface gear, and (d) low Input F and longline gear.

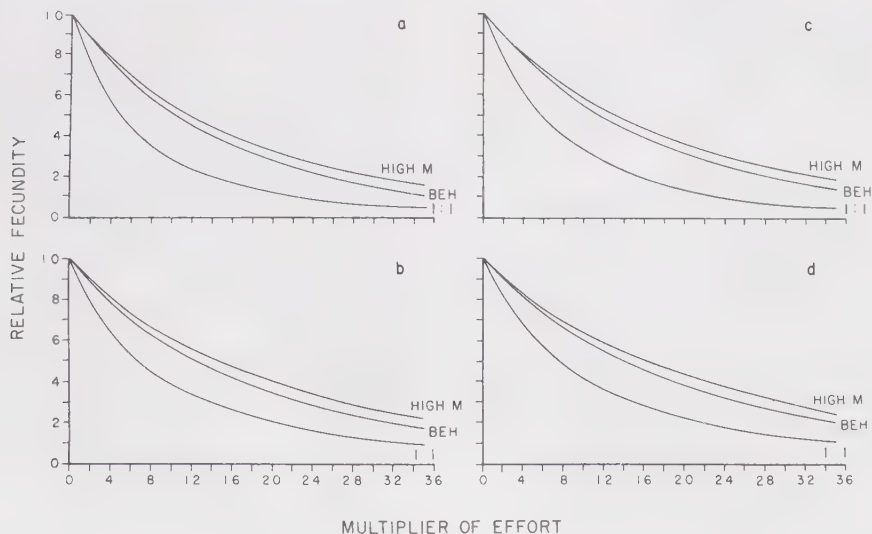


FIGURE 12.—Estimates of relative stock fecundity at size at recruitment at the time of the study as a function of fishing effort, fecundity index, and sex ratio hypothesis: (a) high Input F and fecundity index I, (b) high Input F and fecundity Index II, (c) low Input F and fecundity index I, and (d) low input F and fecundity index II.

With the above results in mind, we developed a computer simulation model to examine the inter-relationships of: 1) patterns of movement of fish; 2) patterns of recruitment (i.e. by area), and 3)

fishing strategy for two gear types (surface and longline) fishing alone or together on the same population.

The model is general in that it allows the user to

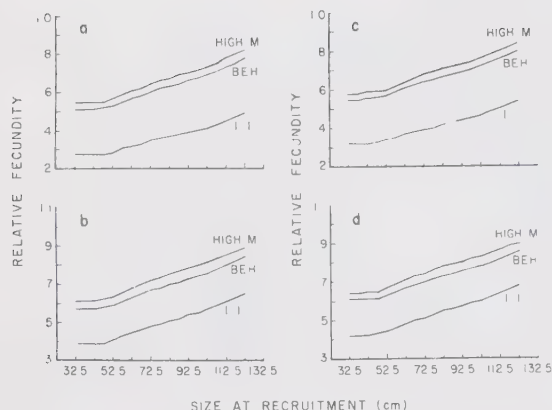


FIGURE 13.—Estimates of relative stock fecundity at level of fishing effort at the time of study as a function of size at recruitment, fecundity index, and sex ratio hypothesis: (a) high Input F and fecundity index I, (b) high Input F and fecundity index II, (c) low Input F and fecundity index I, and (d) low Input F and fecundity index II.

specify the nature of movements, locations of recruitment, parameters of growth, and natural fishing mortality.

We crudely represented the eastern Pacific Ocean with the grid of 5° square areas shown in Figure 14. The number of fish of a specific age in each cell at time t is given by the vector

$$N_t = AS_t N_{t-1} \quad (5)$$

where N_t (112×1) has elements $(n_i)_t$ equal to the number of fish in cell i at time t , S_t (112×112) is a diagonal matrix with elements $(s_{ii})_t$ equal to the survival rate of fish in cell i from time $t-1$ to time t , A (112×112) is a probability transfer matrix with elements (a_{ij}) equal to the probability of a fish in cell j moving to cell i , and where N_0 (112×1) has elements $(n_i)_0$ equal to the number of recruits in cell i . Five consecutive year classes are in the system at a time.

For our work we specified A , the transfer matrix, by the assumption that for any cell the probabilities of fish remaining stationary and moving to each of eight adjacent cells is the same, i.e., $1/9$. Any other transfer has zero probability. This general rule is modified as follows:

1) Probabilities of remaining stationary in cells adjacent to the shore are augmented by the sum of probabilities of those movements which would otherwise put fish on land and the probability of occurrence on land is zero.

		COLUMN													
ROW		1	2	3	4	5	6	7	8	9	10	11	12	13	14
		1	2	3	4	5	6	7	8	9	10	11	12	13	14
2		15	16	17	18	19	20	21	22	23	24	25	26	27	28
3		29	30	31	32	33	34	35	36	37	38	39	40	41	42
4		43	44	45	46	47	48	49	50	51	52	53	54	55	56
5		57	58	59	60	61	62	63	64	65	66	67	68	69	70
6		71	72	73	74	75	76	77	78	79	80	81	82	83	84
7		85	86	87	88	89	90	91	92	93	94	95	96	97	98
8		99	100	101	102	103	104	105	106	107	108	109	110	111	112

FIGURE 14.—Representation of eastern Pacific Ocean. Each cell represents a 5° square area. Hatched cells represent land. Column 1 is western boundary and Column 14 is eastern boundary. Row 1 is northern boundary and row 8 is southern boundary.

2) Probabilities projecting beyond the northern and southern edges are similarly absorbed on the boundaries.

3) In cells of rows 2 and 7, probabilities of moving toward rows 1 and 8 are decreased by half with the probability of remaining stationary increased by a like amount. This is an attempt to simulate a stock encountering increasingly marginal conditions as the northern and southern boundaries are approached.

4) Probabilities of remaining stationary on the western edge are augmented by the probability of returning from beyond the boundary in a single time interval. The remainder of the fish that move beyond the western boundary are lost to the system.

The speed of dispersion is controlled both by A and the time interval. The time interval was 3 mo for this study. The combination of A as defined and time interval of 3 mo allows a fish to travel a maximum of 1,200 mi in a year. Only 1 out of 820 surviving fish that begin the year in the center of the grid travel 1,200 mi in a year. These relatively slow random movements seemed reasonable, based on the results shown in Bayliff and Rothschild (1974) and recent results of IATTC tagging studies (Inter-American Tropical Tuna Commission³).

Two alternative recruitment models were examined. For the first, denoted as inshore re-

³Cited with permission of M. Clifford Peterson, Acting Director of the Inter-American Tropical Tuna Commission. From the Inter-American Tropical Tuna Commission Bi-monthly Report, March-April 1976:8-13.

recruitment, recruits are divided equally among the five cells 51, 52, 69, 83, and 84, which resemble the recruitment areas proposed by Fink and Bayliff (1970). For the other alternative, denoted as uniform recruitment, recruits are divided equally among all cells except those on the boundaries or on land. Total annual recruitment is 100 fish. We assumed 1) that fish are 1 yr old when recruited, 2) growth proceeds according to the von Bertalanffy curve of LeGuen and Sakagawa (1973), and 3) the coefficient of instantaneous natural mortality is 0.8 on annual basis and is independent of time and location. Fish >6 yr old (175 cm) were removed from the system. Consequently, under constant conditions the fishery reaches equilibrium in 5 yr. The system was always run for 5 yr before an experiment was begun.

We first examined the effects of sampling location, dispersal, and location of recruitment on age distribution and the resulting apparent rate of natural mortality obtained from unbiased samples from an unfished population. Mortality was estimated with the standard linear regression model ($\ln N_t = \ln N_0 - Mt$) from the age distribution of fish in each cell. It is assumed that mortal-

ity is constant after full recruitment, and that the modal age represents first age of full recruitment. The results reveal that M is usually overestimated as would be expected when fish emigrate from a sampled area (Figure 15). Estimates of M tend to be relatively high near areas of spawning with inshore recruitment. In the case of uniform recruitment, estimates of M tend to be highest on the western boundary where fish are lost to the system. Modal age tends to increase in a westerly direction for inshore recruitment and stay relatively constant for uniform recruitment (Figure 15). The modal size of actual catches of surface-caught yellowfin tuna in the eastern Pacific increases in a westerly direction (Figure 16). Although the surface fishery probably does not take an unbiased sample of the size distribution of the population, the data are suggestive of reduced recruitment in the western areas.

We simulated a 20-yr hypothetical yellowfin tuna fishery to examine interactions among a longline fishery, inshore surface fishery, ocean-wide surface fishery, and ocean-wide surface fishery that does not heavily exploit young fish as follows:

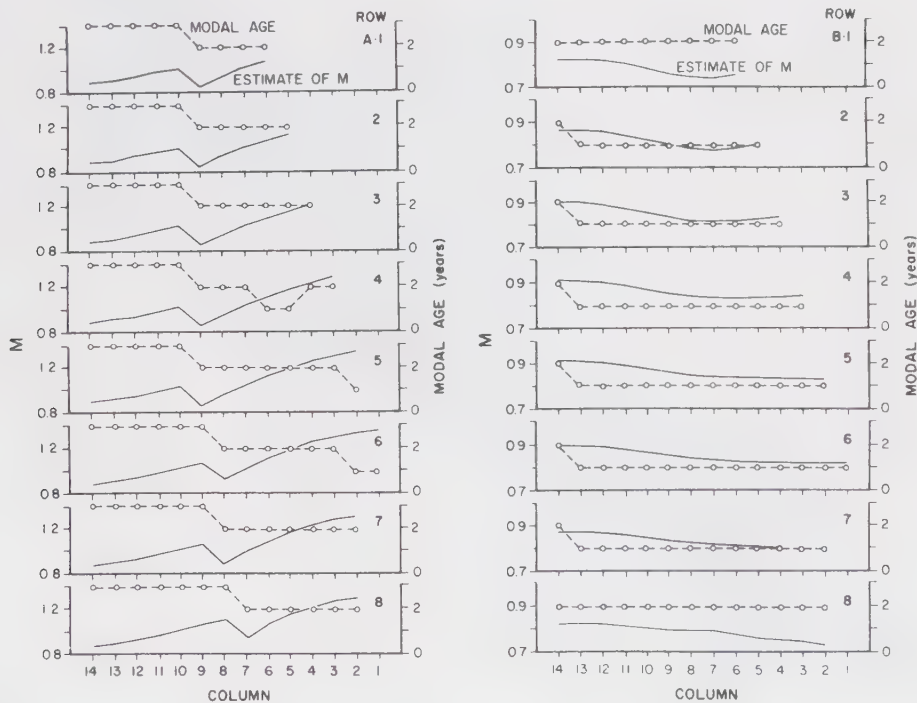


FIGURE 15.—Estimates of coefficient of instantaneous natural mortality on annual basis (M) and modal age of yellowfin tuna by row and column: (A) inshore recruitment, and (B) uniform recruitment.

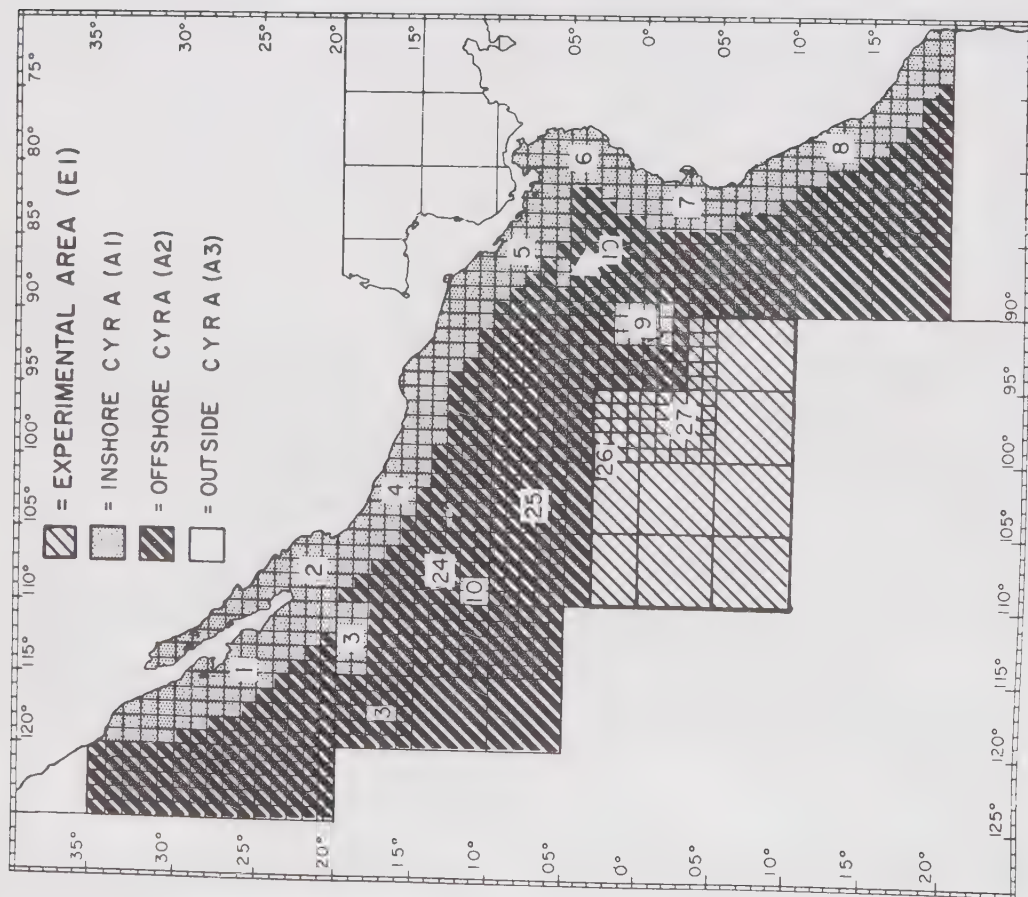
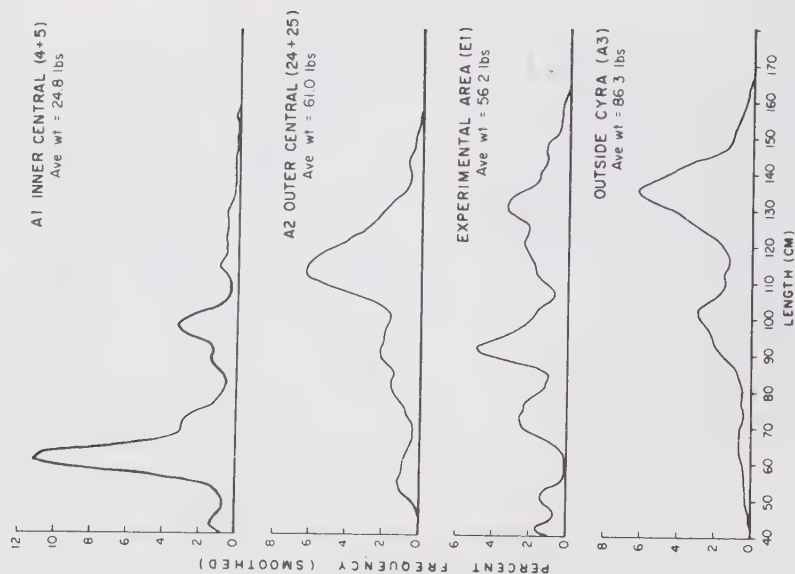


FIGURE 16.—Taken from the Inter-American Tropical Tuna Commission (1974): (a) the eastern Pacific Ocean showing areas A1, A2, and A3. The numbers within the areas designate subareas used for size composition studies, and (b) length-frequency distribu-



tion of yellowfin tuna in the inner area (areas 4 and 5), the outer area (areas 24 and 25) of the central region of the CYRA (Commission Yellowfin Regulatory Area), in the experimental area (EI), and in the area to the west of the CYRA (A3).

1) For the first 5 yr only longliners fished and only in rows 5 to 8.

2) For the next 5 yr, this longline fishery was augmented with surface gear in all cells adjacent to the coast.

3) Next, exploitation by the surface gear was expanded to include all cells for 5 yr.

4) Finally, for the last 5 yr, age specific surface fishing mortality was reduced by 75% for fish <2.5 yr of age because much of the surface catch of yellowfin tuna in offshore areas of the eastern Pacific comes from schools associated with porpoise. Typically, porpoise schools contain few yellowfin tuna <2.5 yr of age (Calkins 1965).

Steps 1, 2, and 3 resemble the sequence of events in the eastern Atlantic fishery for yellowfin tuna. Yellowfin tuna first were exploited in a significant fashion by longliners in a 10° band along the equator, then a nearshore surface fishery became significant, and in recent years some exploitation by surface gear in offshore areas has occurred. To our knowledge, step 4 has not occurred in the Atlantic. Age-specific fishing mortality rates similar to those by surface gears estimated by Lenarz et al. (1974) for the Atlantic yellowfin tuna fishery were used (Table 5). The Ricker yield equation was used to calculate yield for each time-area stratum.

Total yields per recruit were calculated and are shown in Figure 17. Yields per recruit are quite similar for both recruitment models except near shore, where yield per recruit was considerably higher for the inshore recruitment model than for the uniform recruitment model. The difference in yield per recruit between the two models decreases slightly as time increases. Yield per recruit closely approached equilibrium yield within 3 yr after a change was made in the fishery. Total equilibrium yield per recruit with an inshore surface fishery

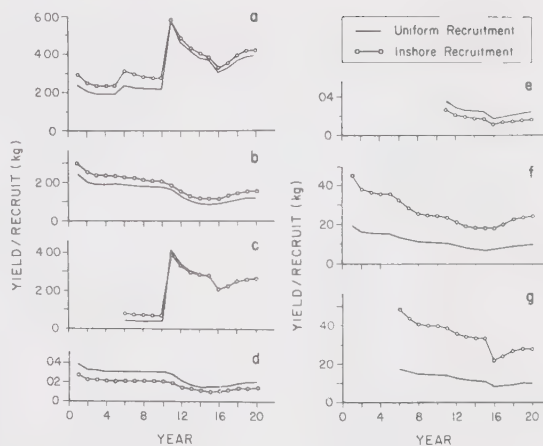


FIGURE 17.—Yield per recruit of hypothetical yellowfin tuna fishery: (a) total, (b) longliners in all areas, (c) surface gear in all areas, (d) longliners in cells 71 and 85, (e) surface gear in cells 71 and 85, (f) longliners in cells 69, 84, and 97, and (g) surface gear in cells 69, 84, and 97.

and longline fishery was about 17% higher than with a longline fishery alone, 54% higher with a uniform surface fishery than with only a longline and inshore surface fishery, and increased by 9% when F for small fish was reduced by 75%. Under the assumption that the catchability coefficient is independent of area, the surface fishery increased its equilibrium yield per recruit about fourfold by increasing its effort about 12-fold when it expanded into offshore waters. The same action decreased yield per recruit to the longliners by about 55%.

We next examined the potential yield per recruit to longliners in rows 5, 6, 7, and 8 by starting a longline fishery with the age-specific F vector multiplied by the scalar 0.3 and then multiplying by 1.3 each year afterward. Yield per recruit appears to approach an asymptote of about 6 kg for inshore recruitment and 5 kg for uniform recruitment (Figure 18). The reduction in catch per recruit per effort by fishing is not significantly affected by choice of recruitment model. Even though catch per recruit per effort at high levels of effort was only about 20% of that at the beginning of exploitation, overfishing in a yield-per-recruit sense did not occur. Average size of fish in the catch was not significantly affected by the recruitment model, and decreased from about 50 to 30 kg with increased fishing effort (Figure 18).

A simulation for an inshore surface fishery indicated an asymptotic production curve with a

TABLE 5.—Estimates of age-specific F on an annual basis used as baseline for simulation. See text for modifications of mortality rates during simulation.

Age (yr)	Longline gear	Surface gear	Surface gear with reduced F
1.0	0.00	0.30	0.08
1.5	0.00	0.30	0.08
2.0	0.05	0.22	0.06
2.5	0.15	0.20	0.20
3.0	0.25	0.18	0.18
3.5	0.35	0.30	0.30
4.0	0.45	0.35	0.35
4.5	0.40	0.42	0.42
5.0	0.40	0.27	0.27
5.5	0.20	0.20	0.20
6.0	0.05	0.15	0.15

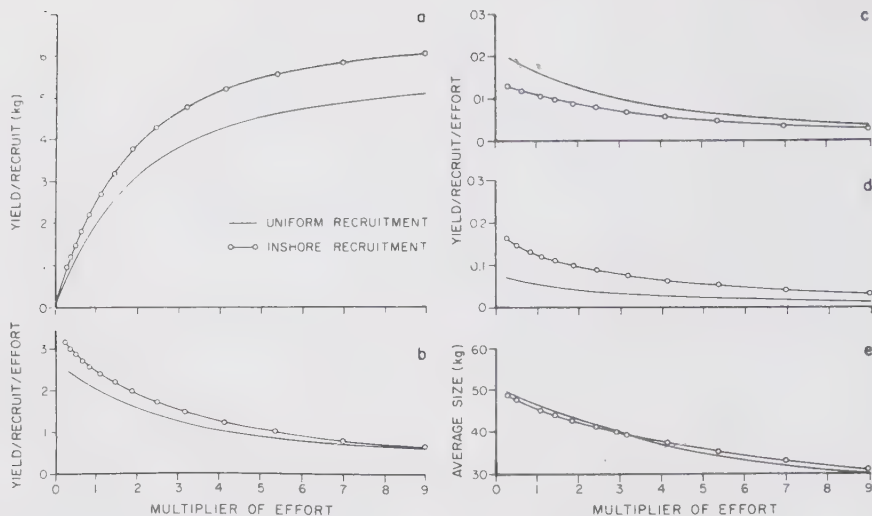


FIGURE 18.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical longline fishery: (a) total yield per recruit, (b) total yield per recruit per effort, (c) yield per recruit per effort in cells 71 and 85, (d) yield per recruit per effort in cells 69, 84, and 97, and (e) average size in all squares.

maximum yield per recruit of about 1.4 kg for uniform recruitment and 2.2 kg for inshore recruitment (Figure 19). Catch per recruit per effort was reduced by about 75% under both alternatives. The ratio of maximum yield per recruit for a longline fishery to an inshore surface fishery was about 2.7 for inshore recruitment and 3.4 for uniform recruitment. Average size of fish in the catch was about 2 kg higher for uniform recruitment than for inshore recruitment and decreased from 16 or 18 kg to 8 or 11 kg with increased fishing effort (Figure 19).

Simulation of a uniform surface fishery revealed that choice of recruitment model had an insignificant effect on yield per recruit, catch per recruit per effort, and average size of catch, except that catch per recruit per effort in the nearshore area was relatively high for inshore recruitment (Figure 20). A 75% reduction in F for fish <2.5 yr old had considerable effect on the results. Maximum yield increased from about 5.1 to 6.9 kg when F was reduced. Both yield curves are dome-shaped. Catch per recruit per effort became relatively higher at high levels of effort when F was reduced. As expected, average size was considerably higher for reduced F .

With inshore recruitment, maximum yield per recruit changes from about 2.2 kg for an inshore fishery (Figure 19) to about 5.1 kg for a uniform

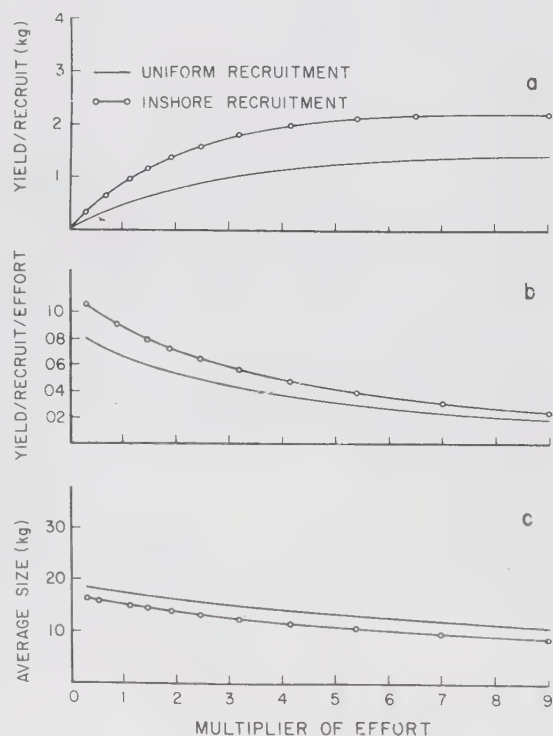


FIGURE 19.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical inshore surface fishery: (a) yield per recruit, (b) yield per recruit per effort, and (c) average size of fish in catch.

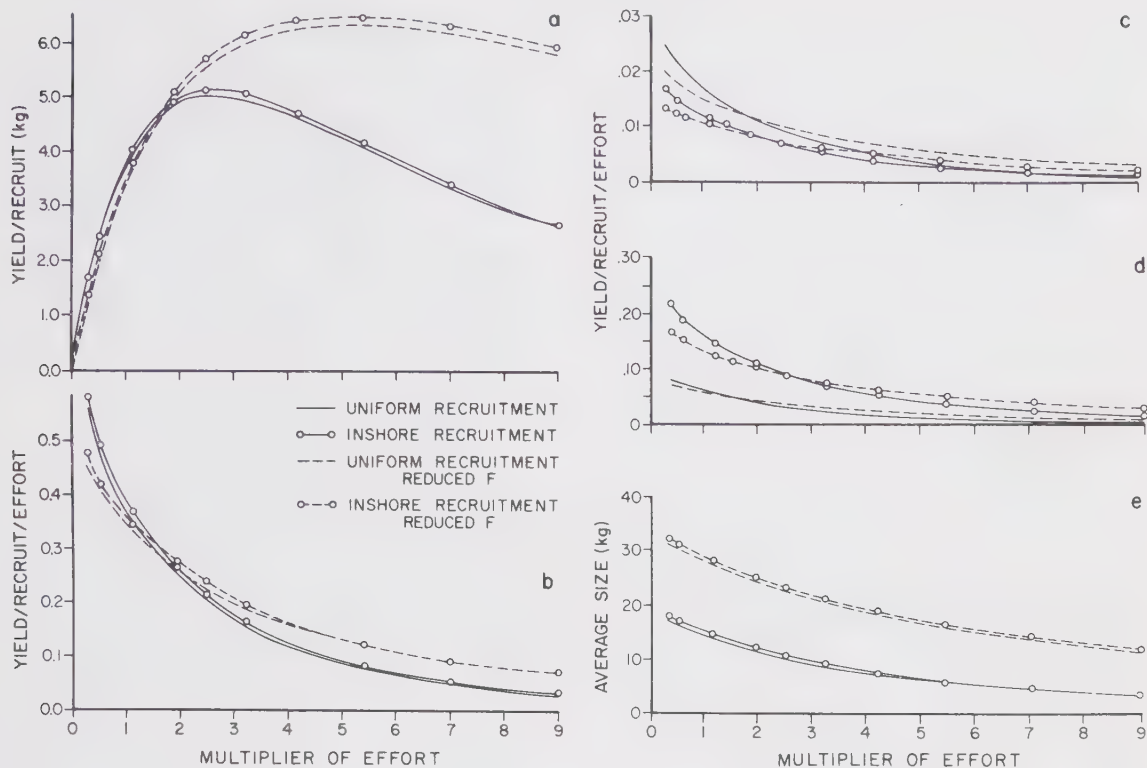


FIGURE 20.—Yield per recruit, yield per recruit per effort, and average size of catch for hypothetical uniform surface fishery: (a) yield per recruit, (b) yield per recruit per effort, (c) yield per recruit per effort in cells 71 and 85, (d) yield per recruit per effort in cells 69, 84, and 97, and (e) average size of fish in catch.

fishery (Figure 20). With uniform recruitment, maximum yield per recruit changes from about 1.4 kg for an inshore fishery to about 5.0 kg for a uniform fishery.

The results of this section indicate that the pattern of recruitment is primarily of interest for examining the potential of a nearshore surface fishery to a surface fishery that exploits the entire area or a longline fishery. The presence of some small yellowfin tuna in length-frequency data for offshore areas from the eastern Pacific fishery (Figure 17) reveals that some recruitment occurs offshore. Recruits apparently are not highly available to surface fishing offshore because most yellowfin tuna are caught in schools associated with porpoise. Such schools normally contain only low percentages of small yellowfin tuna. A well-designed tagging study could provide estimates of the exploitation rate by size for yellowfin tuna in the offshore areas. Until the pattern of recruitment is determined, it will be necessary to continue estimations of relative production to

longliners, inshore surface gear, and offshore surface gear in an empirical fashion.

We examined only one reasonable example of an infinite number of possible configurations of the transfer matrix A and time interval. Further use of the model should include a sensitivity analysis of the results to choice of A and number of cycles per year.

SUMMARY AND CONCLUSIONS

This paper examines three aspects of dual fisheries (surface and longline) on yellowfin tuna. Models of yellowfin tuna fisheries are developed to evaluate possible effects of unknown components of the biology and behavior on the fisheries. The results, while not conclusive because of insufficient knowledge, indicate the magnitude of the effects of those factors which were examined.

We present evidence that not all yellowfin tuna are equally available to longline and surface fisheries in the Pacific Ocean. We show that three

much effect on decisions concerning minimum size regulations. If fish are equally available to both gear types, yield per recruit is higher to a longline fishery than to a surface fishery, but is higher for the combined gears than to either gear fishing alone.

We also note that there is considerable evidence that large females of all commercially important *Thunnus* are caught in fewer numbers than large males. The effect of this phenomenon on yield per recruit and relative stock fecundity was examined for Atlantic yellowfin tuna. When plotted against fishing effort, yield per recruit is more dome-shaped when the sex ratio is 1:1, as is usually assumed, than when the sex ratio is as observed. Changes in size at recruitment also have a greater effect on yield per recruit when the sex ratio is 1:1 than when the sex ratio is as observed. Competition between longline and surface fishing is more intense when the sex ratio is 1:1 than otherwise. The fishery has a greater effect on stock fecundity if the sex ratio is 1:1 instead of that observed.

Tagging studies of yellowfin tuna in the eastern Pacific indicate that movements are fairly slow compared with more highly migratory species such as albacore and bluefin tuna and have not produced any clear-cut evidence of a definite migration pattern. Size composition of the catch suggests that recruitment to the fishery occurs mainly along the coast of Central America. A simulation model was developed for the eastern Pacific to examine the interrelationships of patterns of movements of fish, patterns of recruitment, and fishing strategy. It was assumed that movements were random and recruitment occurred either along the coast or throughout the eastern Pacific. The results indicate that either pattern of recruitment could allow the increased catch observed in the Pacific as the surface fleet moved offshore. However, the pattern of recruitment does affect the potential yield per recruit of a nearshore surface fishery relative to a surface or longline fishery that exploits the entire area. Both choices of recruitment models resulted in an asymptotic relationship between yield per recruit and effort for a longline fishery over the range of effort examined. Overfishing in a yield per recruit sense did not occur, even though catch per effort decreased by 80%. Approximately the same results were obtained for an inshore surface fishery. However, curves of yield per recruit plotted

The study reveals several biological and behavioral parameters which, because of lack of knowledge or information, are rarely considered but do appear to have a significant effect on some aspects of the dynamics of yellowfin tuna fisheries. Tagging and fecundity studies are suggested in order to fill these gaps. Perhaps as important, other aspects of the dynamics of yellowfin tuna fishing appear to be insignificantly affected by the examined parameters.

ACKNOWLEDGMENTS

This study was stimulated by Brian J. Rothschild, who has had a long interest in the interactions between longline and surface fisheries for tunas. The work benefited from discussions with Rothschild and William W. Fox, Jr. of the Southwest Fisheries Center La Jolla Laboratory; William H. Bayliff and Patrick K. Tomlinson of the Inter-American Tropical Tuna Commission, La Jolla, Calif.; Allan Fonteneau of the Centre de Recherches Oceanographiques, Abidjan, Ivory Coast; and Frank Mather III of the Woods Hole Oceanographic Institution. Many of the computer runs were made by Atilio Coan and Kenneth Brenneke of the Southwest Fisheries Center La Jolla Laboratory. We thank William H. Bayliff, Jerry Wetherall of the Southwest Fisheries Center Honolulu Laboratory and John P. Wise, National Marine Fisheries Service, Washington, D.C., for reviewing the paper. We owe considerable thanks to an unnamed referee who made many useful suggestions and to Lorraine Prescott for her patient and excellent typings of several versions of this paper.

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POPULATION ESTIMATES FOR THE WANING YEARS OF THE PACIFIC SARDINE FISHERY

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ABSTRACT

New sardine (*Sardinops sagax caerulea*) population estimates for the period 1945 to 1965 are calculated based on a cohort analysis of aged landings data. Three-year-old fish were incompletely recruited after 1953, requiring assumption of age 4 as age of full recruitment. The assumed natural mortality rate (M) was maintained at 0.4 for the entire time series. Landings from waters south of Punta Baja, Baja California, were excluded from the analysis. Biomass estimates are smaller than those previously given but agree well with independent indices of abundance. The new ratio of sardine spawning biomass to CalCOFI sardine larva census is double the previous value. A 95% confidence interval ranges from one quarter to quadruple the estimated biomass. The stock-recruitment relationship shows no curvature for the entire time series taken as a whole, and a purely functional description of the relationship is that mean recruitment only slightly exceeds potential replacement of spawners at all levels of abundance. Population simulations demonstrate this lack of resilience to fishing. Maximum constant fishing pressure that the population could have sustained was about 22% per year ($F = 0.25$). Maximum sustainable yield was about 250,000 tons/year, which is far below previous estimates.

INTRODUCTION

Estimates of Pacific sardine (*Sardinops sagax caerulea*) spawning biomass in California waters for the period 1932 to 1957 were made by Murphy (1966) using cohort analysis. Besides being the basis of most present analyses of the dynamics of the sardine fishery, estimates of spawning biomass from 1951 to 1957 have been used to calibrate larva surveys for estimation of northern anchovy (*Engraulis mordax*) spawning biomass (Smith 1972). As the northern anchovy fishery is now beginning to expand to a level where increased precision in management is necessary, improvement of the anchovy data base is desirable, and therefore, improvement of the sardine population estimates is indicated.

Murphy offered his analysis of the 1952-1960 seasons as a tentative solution and intended that "As more information . . . becomes available, the solution . . . can be re-examined." The last season for which the age composition of the sardine landings was published is 1965, which was also the last year of significant landings in California.

Murphy used landings up to 1960, so the usable time series can be extended another five years by updating his analysis. Other aspects of Murphy's analysis can also bear revision, particularly with regard to the present use of the results, that of anchovy biomass estimation. Murphy showed that a natural mortality rate of $M = 0.4$ is our best estimate, but for the time series subsequent to 1950, he preferred to double this value to $M = 0.8$ in order to obtain a trend in population sizes which agreed with the egg counts obtained from CalCOFI surveys. Since we are now using Murphy's estimates to calibrate those surveys, the process is suspiciously circular, and consistent use of the best estimate of $M = 0.4$ will preserve independence of the data sets. Age of full recruitment is another assumption that can bear examination and possible revision. Finally, Murphy included the Cedros Island catch in his landings data, which undoubtedly included large amounts of fish from the southern sardine stock that may never have been available in California. Since the northern anchovy central subpopulation has a southern boundary in the vicinity of Punta Baja, Baja California, estimation of biomass by comparing anchovy and sardine spawning products requires that the sardine biomass estimates be based on a similar area. Only sardine landings presumably caught north of Punta Baja will be considered in this analysis.

DATA

The basic input data to a cohort analysis are aged landings (Table 1). For the seasons before 1951, the catch data in Murphy's Table 13 are used. For the period 1951 to 1960, aged landings were recalculated from information in Wolf (1961) and from estimates of total tonnages landed in various regions of the fishery (Table 1). Age compositions for the 1961 to 1965 season were obtained from the individual landings reports (Daugherty and Wolf 1964; Kimura and Blunt 1967; Blunt and Kimura 1966; Kimura and Blunt 1971; Blunt and Kimura 1971; listed in order). Aged landings for each region were modified according to revised total tonnages obtained from various sources. In the late 1950's and early 1960's, sardine catches made out of season (i.e. in the "inter-season") were not included in the landings reports, so aged landings were increased according to the tonnages reported in the California Department of Fish and Game Marine Fish Catch Reports. The aged landings for 1965-

TABLE 1
Pacific Sardine Landings.

Season	Landings (short tons)				Aged landings (1,000 fish)						
	Central California	Southern California	North Baja California	Total	O	I	II	III	IV	V+	Total
1950-51*	46,426	306,662	—	353,088			1,129,439	996,899	391,172	90,704	2,608,214
1951	15,679	113,125	16,022	144,826		13,908	69,624	778,877	179,837	79,603	1,121,849
1952	49	5,662	7,971	13,682		871	4,604	20,533	50,771	17,020	93,799
1953	58	4,434	12,303	16,795		2,150	5,928	35,025	10,812	49,606	103,521
1954	856	67,609	11,694	80,159	3,833	3,011	203,058	228,849	72,644	113,525	624,920
1955	518	73,943	3,828	78,289		11,340	71,827	268,656	140,996	57,483	550,302
1956	63	33,580	12,290	45,933			20,080	90,154	115,587	41,410	267,231
1957	17	22,255	8,932	31,204	4,393	56,544	57,910	77,527	35,141	41,120	272,635
1958	24,701	79,270	16,527	120,498		131,713	812,293	252,062	37,556	23,653	1,257,277
1959	15,645	21,538	14,140	51,323		67,723	299,484	150,980	18,231	2,112	538,530
1960	2,076	26,690	10,148	38,914		3,523	107,991	164,380	56,161	4,457	336,512
1961	2,211	23,313	1,587	27,111	1	369	11,029	34,613	76,001	45,837	167,850
1962	1,206	2,897	2,592	6,695		6	2,290	13,814	15,827	10,608	42,545
1963	1,008	2,459	2,521	5,988		1,458	4,332	9,202	13,291	11,347	39,630
1964	307	5,984	476	6,767	98	274	7,591	21,838	12,442	10,631	52,874
1965	70	909	431	1,410			730	523	2,250	4,765	8,268

*Landings prior to 1950 are as reported in Murphy (1966).

66 were poorly sampled and incomplete; therefore for this season the southern California age composition was assigned to all California landings and the Baja California interseason age composition was assigned to all Baja California landings. The amount of fish caught in northern Baja California waters before 1961 was estimated by multiplying the Baja California tonnage by the combined Ensenada and San Quintin percents of total landings in Murphy's Table 7. For 1961 through 1963, Murphy's Table 8 was used in similar fashion. The 1964 and 1965 landings reports say that "insignificant" amounts of the sardines processed in Ensenada were caught locally, which I have interpreted as 10%, for lack of a better estimate.

In most of the aged landings reports, no distinction is made between Cedros Island-area catch and Ensenada-area catch, which becomes a problem in 1961 through 1965, when large amounts of fish caught in central Baja California were shipped to Ensenada for processing and appear in the Ensenada landings estimates. Length frequencies for the two areas differ considerably in some years, with Ensenada fish being generally smaller than southern California fish and with Cedros Island fish being smaller yet (Blunt and Kimura 1966; Kimura and Blunt 1967). Two sets of landings data for 1961 to 1965 were analyzed separately, one assigning the Baja California age composition to the Ensenada catch, and the second assigning the southern California age composition to the Ensenada catch. As the true Ensenada age composition is likely to be intermediate between the two estimates, the estimates made by separate cohort analyses should correspondingly bracket the estimate that would have been obtained using the true Ensenada age composition.

ESTIMATION OF FISHING MORTALITY RATES

Cohort analysis, as described by Tomlinson (1970), was used to estimate fishing mortality rates from the aged landings data. Natural mortality is assumed to be $M = 0.4$, based on the review of sardine natural mortality rate given by Murphy (1966). Age 4 and older fish are considered fully recruited, so catch ratios of the form

$$R_i = \frac{\sum_{j=5}^{\infty} C_{i+1,j}}{\sum_{j=4}^{\infty} C_{i,j}}$$

where i is fishing season, and j is age, were used to connect the time series of fully recruited ages. A backward solution estimated F_i , given F_{i+1} and R_i , and due to the assumption of full recruitment, the F_i so estimated for age-4+ fish was assigned to the age-5+ fish in the same season, allowing the process to be repeated for the next earlier cohort. The assumption of full recruitment at age 4 was necessitated by that being the oldest age for which older fish were still sufficiently abundant to obtain catch ratios that were relatively unaffected by sampling variation. Solution for the younger, partially recruited ages was also done by the method described by Tomlinson (1970). Murphy's solutions were based on mathematically equivalent calculations; therefore, the method itself is not a source of difference in the results given here.

The fishing mortality rate for fully recruited ages in 1965 was arbitrarily set at $F_{1965} = 0.6$ to initiate the time series. Since this is purely a guess, the 1965 and 1964 values must be considered inaccurate. Fortunately, backward solution has the property of convergence (Tomlinson 1970; Jones 1961), wherein each successive earlier estimate is less affected by error in later estimates and tends toward a fixed value, which can be called its

true value if all assumptions are valid. Thus, the F_i estimates for $i = 1963$ and earlier may be considered to be reasonably independent of the initial guess.

For the 1950's, fishing mortality rates estimated from the new data and assumptions tend to be two to three times larger than those estimated by Murphy (Table 2). After 1953, 3-year-old fish are not fully recruited, averaging 69% the fishing mortality rate of older fish from 1954 to 1963. Violation of the assumption of full recruitment caused progressive underestimation of F for "fully recruited" ages in Murphy's solution. This also explains why Murphy had to choose an inordinately large value of M and of F_{1960} to initiate his solution. The present solution gives results back to 1945, where the recalculation converges with Murphy's solution. Both previously discussed methods of assigning age composition to the later Mexican catches give approximately the same results (Table 2), except for the younger ages after 1961.

An additional factor tending to keep Murphy's estimates of fishing mortality low is his inclusion of catches from the more lightly exploited southern stock in central Baja California. As these southern landings become an

TABLE 2
Pacific Sardine Fishing Mortality Rates.

Age Season	$M = 0.4$			Murphy (1966) $M = 0.4$		Murphy (1966) $M = 0.8$	
	2	3	4+	2	3+	2	3+
1945-46	0.631	1.017	1.179	0.553	1.170		
1946 ...	0.496	0.752	0.595	0.476	0.589		
1947 ...	0.285	0.415	0.628	0.194	0.389		
1948 ...	0.314	0.313	0.326	0.346	0.192		
1949 ...	0.514	0.669	1.054	0.430	0.619		
1950 ...	0.455	1.148	1.207	0.394	0.796		
1951 ...	0.349	0.880	0.876		0.681	0.039*	
1952 ...	0.014	0.204	0.151		0.113	0.002	0.036
1953 ...	0.007	0.179	0.196		0.143	0.000	0.042
1954 ...	0.229	0.555	0.901		0.340	0.103	0.245
1955 ...	0.257	0.691	1.108		0.203	0.118	0.376
1956 ...	0.096	0.773	1.002			0.044	0.431
1957 ...	0.127	0.841	1.113			0.014	0.476
			(1.112)†				
1958 ...	0.922	1.790	2.424			0.690	1.218
	(0.916)	(1.783)	(2.417)				
1959 ...	0.503	0.553	0.808			0.406	0.783
	(0.501)	(0.546)	(0.798)				
1960 ...	0.592	0.756	0.528				1.359
	(0.565)	(0.752)	(0.516)				
1961 ...	0.128	0.490	1.440				
	(0.086)	(0.388)	(1.465)				
1962 ...	0.038	0.292	0.562				
	(0.002)	(0.358)	(0.445)				
	(0.149)	(0.079)	(0.683)				
1964 ...	1.549	1.353	0.896				
	(2.145)	(1.739)	(0.932)				
1965 ...	0.5	0.6					

*Estimated from Murphy's (1966) Tables 13 and 14.

† Parentheses indicate results of assigning southern California age composition to the Mexican landings in seasons 1962 through 1965.

increasing fraction of the total catch, the age composition of the southern stock, which reflects less fishing mortality, progressively dominates the cohort analysis, producing underestimated F and overestimated population size for the northern fishery.

ESTIMATION OF BIOMASS

Murphy's (1966) procedure was followed as much as possible, but information on actual weights of individual age groups in the catch compositions is lacking, forcing the use of approximate methods. Since total catch weight and landings by age in number are known (Table 1), age groups were assigned the weights at age given in Murphy's Table 17, and the total catch weight was apportioned by the estimated percentage weight composition, giving estimated landings by age in tons. These landings were then divided by the exploitation rate to give age group biomasses at the beginning of the season. Population biomass was then obtained by summing over age groups (Table 3). Murphy's calculations of spawning biomass for years before 1951 included only half of the 2-year-old fish. The present estimates include all of this age group for the entire time series, under the assumption that 2-year-olds are inherently capable of spawning and therefore constitute a "potential" spawning biomass. This simplification avoids the abrupt change of methods found in the previous estimates. Too little information is available to attempt to define a population size-dependent maturity function.

TABLE 3
Pacific Sardine Biomass and Recruitments.

Year	Adult biomass (10 ³ metric tons) Age 2+		Recruitment Year-class at age 2 (10 ⁶ fish)	
	Present calculation	Murphy's (1966) Table 15	Present calculation	Murphy's (1966) Table 14
1945	720	757	2,385	2,620
1946	566	459	1,625	1,680
1947	405	475	1,667	2,349
1948	740	623	3,875	3,102
1949	793	869	4,261	4,921
1950	780	883	5,690	4,151
1951	277	517	290	2,205
1952	136	503	397	2,494
1953	202	643	972	3,380
1954	239	606	1,197	3,011
1955	170	386	382	935
1956	108	266	264	695
1957	90	192	588*	1,216
1958	177	255	1,586*	2,490
1959	122	172	905*	1,327
1960	88		288	
1961	54		111	
1962	27		74	
1963	21		56	
1964	11		11	
1965	3			

*These recruitments are slightly underestimated due to significant catch of fish at age 1.

Biomass estimates for 1951 and later are much smaller than those calculated by Murphy, as is consistent with the estimates of fishing mortality rate. Despite the poor accuracy of the estimates of fishing mortality rate in 1964 and 1965, the biomasses for those years are undoubtedly extremely small relative to previous years. The two methods of assigning age composition to Mexican landings give nearly identical estimates of biomass, so the solution using Mexican age compositions is presented as the final estimate.

DISCUSSION

Availability at Age

As discussed earlier, Murphy's estimates of fishing mortality rates for the 1950's appear to have been biased downward because he included incompletely available 3-year-old fish in his catch ratios for assumed fully recruited age groups. Thus, the new estimates of fishing mortality rates that are based on an older assumed age of full recruitment are considerably higher because most of the catch ratios are smaller (i.e. catches of year-classes show a larger relative decrease in subsequent years). A comparison of relative availability to the fishery, as measured by the ratio of fishing mortality of ages 2 and 3 fish to "fully recruited" age 4+ fish (Figure 1) shows an interesting trend. Until 1953, 3-year-old fish appear to have been nearly fully available. This group subsequently, with the exception of the 1960 season, underwent a decline in relative availability to 70% in the later 1950's and to less than 50% in the early 1960's. Two-year-old fish show an even more severe drop in relative availability, a decline which also started earlier. From an average of 65% relative availability in the late 1940's, 2-year-olds dropped to 10% relative availability in the 1950's and later, with the exception of the warm-water years, 1958-60.

These trends are remarkably consistent with Felin's (1954) hypothesis concerning the geographic origin of year classes in the later years of the fishery, wherein the later, weaker year classes were thought to be of southerly origin. Now we can further hypothesize that as the fish in the catch were becoming predominantly of southern origin, slow rates of migration into California waters resulted in these fish not being fully available until an older age than was experienced from previous locally produced year classes. Oceanic conditions appear to have influenced this immigration rate as in the case of the warm-water years, when strong northward migration of sardines resulted in greatly increased availability of young fish to the southern California fishery.

Egg and larva surveys have shown little spawning in the Los Angeles Bight since 1951, except during the warm-water years (Kramer 1970). This independent

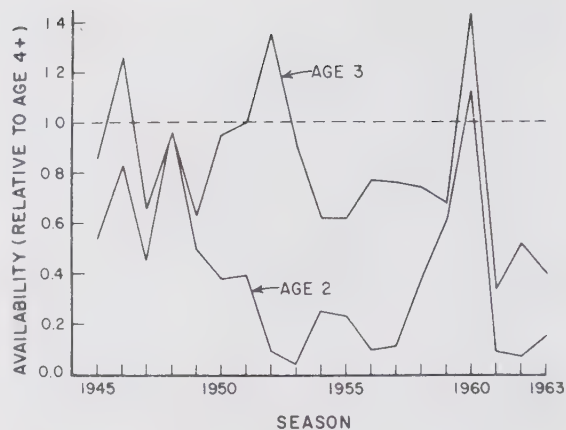


Figure 1. Relative availability of 2- and 3-year-old sardines compared to fully recruited age groups.

source of information strongly supports the above hypothesis, and the occurrence of northerly spawning in the warm-water years also helps explain the high availability of the 1957 and 1958 year classes. At the same time, these conditions of high availability resulted in the fleet generating maximal fishing mortality during this period, with the exploitation rate reaching 80% of fully recruited fish in 1958. It is ironic that the conditions that allowed the fishermen to rejoice at the return of the sardine insured the loss of the fishery by making those same sardines extraordinarily vulnerable to capture.

Biomass

Whereas Murphy's estimates of total biomass (age 2+) show a relatively large population in 1950, dropping to intermediate levels in 1951-1954 and then declining steeply, the present solution shows an extreme drop in biomass after 1950, and a subsequent slower, fluctuating decline (Figure 2). Of course, it must be emphasized that there is a geographic difference between the two population estimates in that the new solution is restricted to the waters north of Punta Baja, approximately the boundary between central and northern Baja California, and that much of the difference in the two solutions may be explainable on this basis alone. However, for examining events in the California fishery, the new solution should be more appropriate. The decline since 1950 has been monitored by three other independent methods, and a comparison of these time series with both Murphy's and the new cohort analysis should be informative. The three independent methods are 1) catch-per-unit-effort (Clark 1956; Klingbeil 1974); 2) night-light surveys carried on by the California Department of Fish and Game (Klingbeil 1974); and 3) egg and larva surveys carried on by CalCOFI.

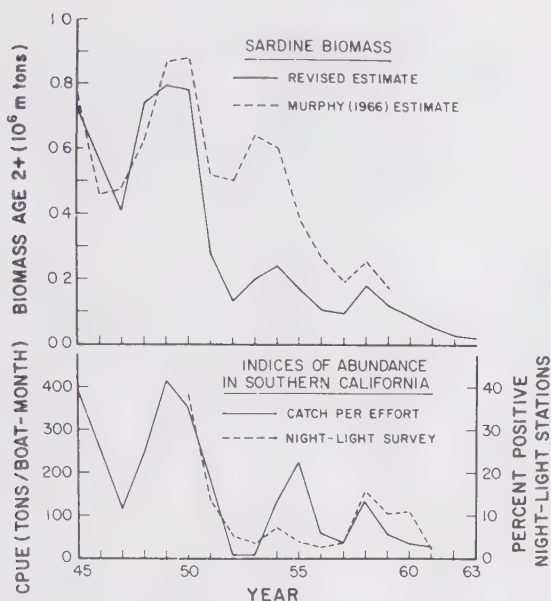


Figure 2. Comparison of sardine biomass estimates and indices of abundance.

Catch-per-unit-effort (CPUE) indices of abundance, particularly when as unrefined as those used in the Pacific sardine fishery, are plagued with systematic errors. MacCall (1976) has shown that the catchability coefficient for available measures of effort in the earlier Pacific sardine fishery tended to vary inversely with biomass, causing decreased sensitivity of CPUE to changes in biomass. Knaggs (1972) documents a wide range of gear improvements in the fishing fleet since 1952. Most of the improvements were in relation to speed and efficiency in the capture and loading of fish. The Puretic power block reduced manpower requirements and operating costs and greatly decreased the duration of a set, allowing more sets to be made on smaller schools. Other improvements resulted in more efficient navigation and location of fish, such as aerial scouting, which takes most of the randomness out of the process of fish location and causes a tendency toward constant CPUE, independent of true abundance. Thus, while CPUE is likely to vary with abundance, it is also likely to underestimate changes in true abundance.

Since most of the landings occurred in the first months of the fishery season after 1944, it is reasonable to compare CPUE with biomass estimates for the beginning of the season. CPUE, in tons per boat-month as given by Clark (1956), and by Klingbeil's (1974) "first approach" (Figure 2), appears to agree somewhat more with the new

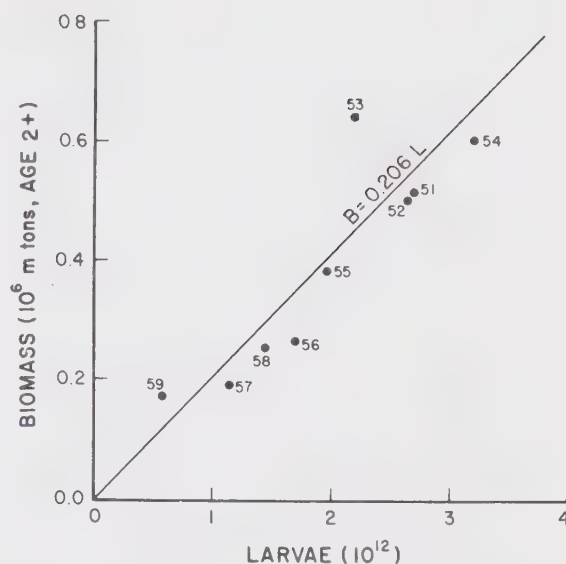


Figure 3. Relationship between sardine spawning biomass and CalCOFI sardine larva census (from Smith 1972).

biomass estimates than with Murphy's estimates. The correspondence is good up to 1952, and the new estimates are much more consistent with the magnitude of the drop in CPUE from 1950 to 1952. The 1953 and 1954 seasons' CPUE are anomalous for both estimates of biomass, although the low fishing mortality rate supports the hypothesis that the stock was not fully available to the fishery. CPUE again agrees well with the new biomass estimates after 1954.

Klingbeil (1974) gives percentage occurrence of sardines at night-light stations as a tentative index of abundance. The index is based on a binomial distribution when fish are abundant, assuming the probability of getting a positive observation is directly related to abundance. However, as abundance becomes small, the probability of obtaining positive observations becomes small, and the distribution becomes approximately Poisson ($N > 100$ and $p < 0.05$), which has the property that the variance is equal to the mean. Thus, the relative precision is poor at low population sizes. Also, pre-recruits accounted for a large number of positive observations, so comparison with abundance estimates is very crude (Figure 2).

Other sources of bias in the night-light index are probable variations in fish behavior, both seasonally and annually. It appears likely that the same factors that may have caused exceptionally high availability of the popula-

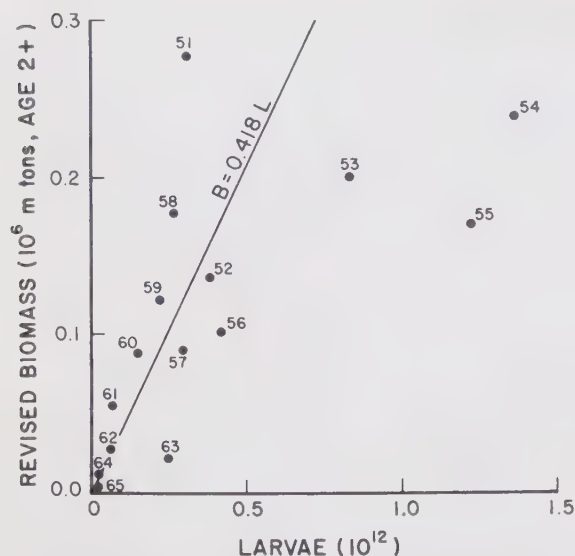


Figure 4. Revised relationship between sardine spawning biomass and CalCOFI sardine larva census for area north of Punta Baja.

tion to the fishing fleet in the warm-water years of 1958-1960 may have resulted in upward bias of the night-light index for those years. Nonetheless, the night-light index shows a large population in 1950, followed by a sharp decline. The 1951, 1954, and 1958 points suggest that abundance in these years may have been on the order of one-third that of 1950, which is much more consistent with the new biomass solution than with the old.

Smith (1972) used the relationship between Murphy's (1966) sardine biomass estimates and the CalCOFI sardine larva censuses to calibrate the CalCOFI anchovy larva censuses. However, Murphy forced his cohort analysis results to agree with the CalCOFI sardine egg censuses, which are highly correlated with the sardine larva censuses. Therefore, the remarkably good relationship between Murphy's estimates and the CalCOFI sardine larva censuses (Figure 3) is somewhat artificial and is not a test of the validity of his biomass estimates. Actually, the relationship is much tighter than should be expected: Taft's (1960) analysis of CalCOFI sardine egg sampling indicated that the variance of a single cruise estimate increases with the mean, so that 95% confidence limits for the mean would be one-half to double the estimated value. Since temporal variability is also extreme, the season estimate is probably relatively less precise than single cruise estimates. Also, in comparing spawning products with cohort analysis abundance estimates, further variability is likely from environmental influences

Table 4
CalCOFI Census of Pacific Sardine Larvae.

Year	TOTAL AREA (Smith 1972)		NORTH OF 30° N (Smith, personal communication)	
	census (10 ⁸ larvae)*	biomass/larva (10 ⁻⁴ tons/larva)	census (10 ⁸ larvae)	biomass/larva (10 ⁻⁴ tons/larva)
1951	2685	0.193	305	0.908
1952	2633	0.191	382	0.356
1953	2189	0.294	732	0.276
1954	3193	0.190	1361	0.176
1955	1959	0.197	1220	0.139
1956	1706	0.156	419	0.258
1957	1137	0.168	293	0.307
1958	1453	0.175	266	0.665
1959	570	0.302	219	0.557
1960	975		150	0.587
1961	642		67	0.806
1962	731		64	0.422
1963	379		248	0.085
1964	505		20	0.550
1965	1098		19	0.179
1966	735		31	
mean		0.207		0.418
standard deviation		0.053		0.251

*Smith (1972) erroneously used units of 10¹² larvae.

on spawning rates. Figure 3 shows none of these properties.

Although the recalculated sardine spawning biomasses are much lower than Murphy's for the period since 1950, the geographical area is also much smaller. For proper comparison, the CalCOFI censuses must also reflect this change in area, and therefore will also be considerably smaller than the previous values (Table 4). The revised relationship between larva censuses and estimated spawning biomass (Figure 4) shows much more scatter than did Smith's (1972) relationship; however, the pattern is very consistent with the sampling properties described by Taft (1960). When the logarithms of the variates are considered (Figure 5), the geometric mean (GM) regression (Ricker, 1973) slope is 0.973. This slope is reasonably close to the value of 1.0, which is characteristic of a proportional relationship between the untransformed variates and is a necessary quality of a good index. The error variance is constant for the log transformation, and the scatter about the regression is about twice Taft's "one-half to double" $s = 0.691$, 95% confidence limits are one-quarter to quadruple.)

Smith (1972) found the relationship

$$B = 0.206 L \quad (s = 0.053)$$

where B is sardine spawning biomass (million tons) from

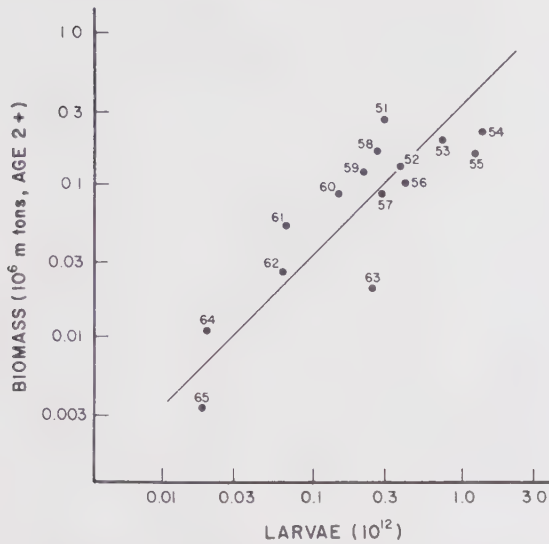


Figure 5. Revised relationship between sardine spawning biomass and CalCOFI sardine larva census, plotted on logarithmic scale.

cohort analysis, and L is CalCOFI larva census (10^9 larvae). The revised relationship (calculated as the mean of the ratios) is

$$B = 0.418 L \quad (s = 0.251)$$

or about double the previous estimate but with much less precision than was formerly attributed to the relationship. Because Smith's (1972) method of calibrating CalCOFI anchovy larva censuses only makes the assumption that anchovies are twice as fecund as sardines, without specifying either actual fecundity, his anchovy biomass estimates are unaffected by this change in sardine biomass calibration.

While showing a large amount of scatter, the CalCOFI sardine larva census estimates agree with the recalculated spawning biomass estimates as much as can reasonably be expected. In this case the cohort analysis was done in ignorance of the larva census values, and the relationship can be used as a validation of results.

Stock-Recruitment Relationship

At low biomass, sardines appear to be fully mature at age 2, but at large biomasses only some of the 2-year-olds are mature. For purposes of this discussion, spawning biomass will be calculated as all fish of age 2 or older, and any lost spawning potential at large biomasses will be subsumed in density-dependent characteristics of the stock-recruitment relationship. Recruitment can be compared with spawning biomass by using Murphy's concept of "potential spawning biomass," being the expected

spawning biomass of a year-class integrated over its lifetime, given particular mortality and growth rates. Murphy's calculation of potential spawning biomass will be modified here: all fish age 2 or older contribute, and the measure of initial year-class strength will be numbers of individuals at age 2 rather than biomass at age 2. The reason for the latter change is that calculation of biomass is dependent upon estimation of the mean weight of an individual in the year class. This, in turn, is strongly affected by the time of year in which most of the 2-year-olds are caught and is, therefore, subject to large and non-relevant sources of variation. Moreover, large fish at age 2 do not necessarily maintain a proportional weight advantage throughout the remainder of their lives. Weights at age are taken from Murphy's Table 16 and will be constant for all levels of biomass. Probable higher growth rates or condition factors when population size is low (MacGregor 1959) are ignored here but could result in as much as a 15% increase in spawning potential.

Previous analyses of the sardine stock-recruitment relationship (Clark and Marr 1955; Radovich 1962; Murphy 1966, 1967) showed density dependence, often by assuming a parabolic or Ricker functional relationship. There is sufficient scatter in the data to fit nearly any type of stock-recruitment function, with no way of determining the true relationship. Other information, such as the geographic composition of the stock (Radovich 1962), can be added to produce a plausible description of the stages in the historical collapse of the fishery. On the other hand, Cushing (1971) concluded that clupeoid stocks tend not to have strong density-dependent regulatory mechanisms, resulting in extreme natural variability and susceptibility to overfishing.

The Pacific sardine has experienced a thousand-fold decrease in abundance since 1932, which makes it necessary to condense the stock-recruitment observations by use of log transformations (Figure 6). Diagonals representing replacement under different fishing mortality rates are plotted for reference. Contrary to previous analyses of the stock-recruitment relationship, this plot shows no functional density-dependent trends whatsoever and agrees with the position of Cushing (1971). There is no increase in recruitment strength relative to parental biomass at low stock sizes, and at every stock size before 1960, recruitments are evenly distributed about the replacement line if there is no fishing mortality. As fishing mortality rate increases, fewer spawnings exceed replacement strength, indicating very little resilience of the population to fishing pressure. For the years 1932 to 1959, the mean replacement success, as measured by $\ln R - \ln P$, is only 0.11, or 12% above replacement at no fishing mortality (the arithmetic mean would be slightly larger). Since year-classes persist for several years and strong year-classes are arithmetically stronger than their loga-

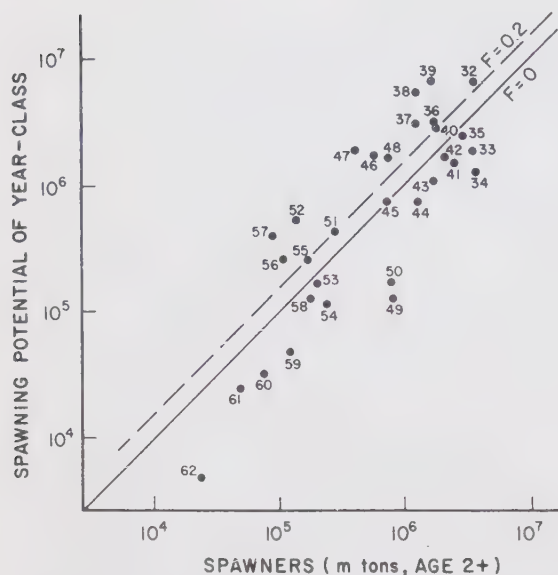


Figure 6. Stock-recruitment relationship of sardine plotted on logarithmic scale.

ritmic values suggest, the reproductive potential may be somewhat higher than the above analysis would conclude. Also, successful reproduction seems to occur in sequences of several years' duration, followed by similar runs of poor reproduction. The duration and timing of these runs has a large effect on potential population growth over long periods of time. These factors will be evaluated by simulation in the next section.

The string of poor recruitments since 1958 is remarkable in its duration and magnitude. The most likely explanation is that the high fishing pressure of the 1950's decimated the northern stock to the point where immigration from the southern stock was making up a large portion of the commercial catch. Consequently, estimates of the size of the northern stock are inflated for purposes of estimating its spawning potential (although they may be fairly realistic as a measure of biomass available to the fishery). Presumably, fish of southern origin are less likely to spawn in the cool waters off California. The record since 1958 is not necessarily a series of spawning failures but may be a series of overestimated spawning biomasses for the northern stock.

Population Simulations

Simulation models of the Pacific sardine stock have been used to answer questions relating to management strategies (Lenarz 1971) and to probable futures of the population (Murphy 1967). These simulations employed the Ricker stock-recruitment relationship given by

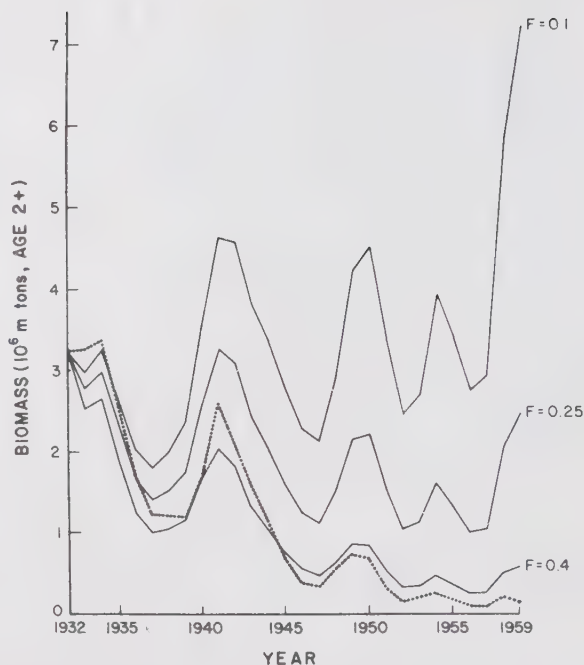


Figure 7. Sardine population simulation results for various rates of constant fishing mortality rates.

Murphy (1966) and reflect the production characteristics of that curve. If the functional stock-recruitment relationship is virtually linear, as is suggested in this paper, the previous simulations are unrealistic and contain a tendency toward an equilibrium which may not, in fact, exist.

The effects of two simple management strategies, constant fishing mortality rate and constant quota, will be examined as they would have affected the actual population from 1932 to 1959, the last potentially peak year of population size. The simulation model recreates annual population age compositions based on spawning rates and natural mortality rates as they historically occurred. Fishing mortality rates (determined by management strategy) are the only source of variation in the model; all other elements are fixed. Observed spawning rates, measured as recruits at age 2 per parental biomass age 2 and older, are employed directly. This method of simulating recruitment makes few assumptions as to the true nature of the stock-recruitment relationship. If any density-dependent compensation actually occurs in this relationship, those simulated will tend to be "optimistic" when the simulated population is larger than the actual population from which the spawning rates were obtained. The simulation begins with the age distribution in 1932 given by Murphy (1966, Table 14) and uses the constant weights at age given in his Table 16. Fish of age

3 and greater are treated as fully recruited to the fishery, and age-2 fish are 50% recruited, suffering one-half the instantaneous fishing mortality rate applying to older fish. A natural mortality rate of $M = 0.4$ is assumed for all ages.

The first simulation (Figure 7) examines population trends under three levels of constant fishing pressure: $F = 0.1, 0.25, \text{ and } 0.4$. The first value allows slow growth, with the population jumping to unreasonably high biomasses in 1958 and 1959 due to the high spawning rates of 1956 and 1957. The second value of $F = 0.25$ causes the population to decline slowly from its peak in the early 1930's, maintaining biomasses between one and two million tons. The third value causes the population to decline to very low levels of about one-half million tons, which must be considered suboptimal. The biomass fell to even lower levels under the actual fishery, giving the simulations an upward bias except for the first few years when the fishing pressure was light and the actual population was larger than the simulation. Thus it appears that $F = 0.25$ is about the maximum constant-fishing pressure that the sardine fishery could have sustained.

An interesting but unrealistic simulation is that of $F = 0$, simulating the growth rate resulting from observed recruitment rates unhindered by fishing or environmental limitation. If the stock-recruitment relationship actually has little or no density-dependent compensation (except at very large population sizes), this growth rate is an approximation of the intrinsic rate of increase (r) in the natural environment. The slope of the logarithm of these simulated population sizes versus time gives an r of 0.082 (8.5%/year). This is considerably less than Murphy's (1967) value of $r = 0.338$, which was based on an extrapolation of his assumed, highly density-dependent Ricker stock recruitment curve to a theoretical zero biomass.

The second simulation holds the annual catch of the fishery constant, approximating a constant-quota system (Figure 8). The simulated population is able to maintain its biomass under a quota of 300,000 metric tons annually but is unable to maintain a quota of 350,000 tons. Due to the "optimistic" bias of the simulation, a safer estimate of maximum sustained yield (MSY) would be 250,000 tons annually. Murphy's (1966) estimate of MSY was 427,000 metric tons (471,000 short tons), which does not seem to have actually been sustainable. The extreme sensitivity of a naturally fluctuating resource to small changes in quota levels indicates the danger of basing management on such an inflexible system. A programmed reduction or cessation of fishing at low biomasses is necessary to provide protection from collapse of an easily overfished resource.

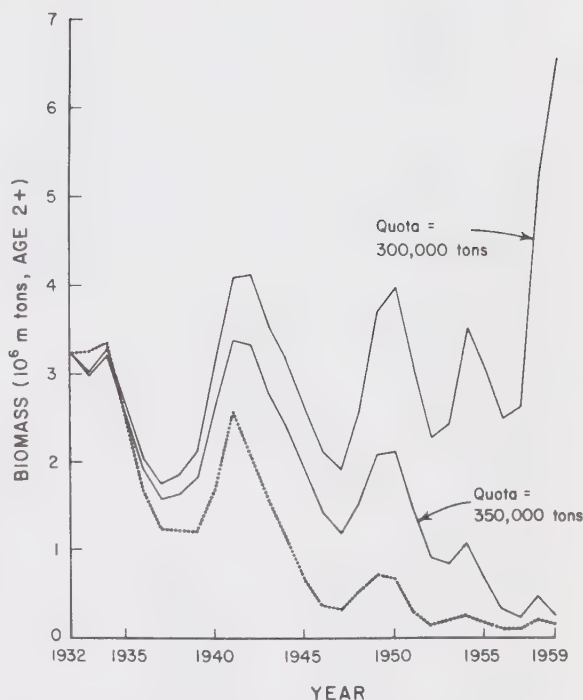


Figure 8. Sardine population simulation results for two levels of annual catch quotas.

This estimate of maximum sustainable yield from the sardine fishery is much smaller than the Gulland potential-yield estimate (Gulland 1970) would give. Using a natural mortality rate of $M = 0.4$ and using the 1932 biomass of 3.2 million metric tons as an estimate of virgin fishable biomass (B_0), potential yield (C_{max}) is estimated to be $0.5 \times 0.4 \times 3.2$ million tons, or 640,000 tons. This is two and one-half times larger than the simulation result and clearly would not be sustainable. The Gulland potential yield estimator appears to require further modification in the case of a naturally fluctuating stock, which may have little density-dependent regulation of recruitment. Two modifications may be suggested: either use as B_0 the smallest population size that has been observed in the virgin state, or use one-half of the Gulland potential yield as a more realistic estimate. For example, the Gulland potential yield from the northern anchovy (*Engraulis mordax*) central stock has been estimated as one to two million tons (MacCall et al. 1976). One-half of this estimate is 500,000 to 1,000,000 tons, which is much closer to estimates of surplus production based on observed growth rates of the population (Radovich and MacCall, this volume), which project an anchovy MSY of approximately 450,000 tons.

CONCLUSIONS

1. A new time series of biomass estimates for Pacific sardine extending to 1963 is presented, based on a cohort analysis of catches from the geographical area associated with the northern stock. The new population estimates are considerably smaller than those previously published and are, moreover, in better agreement with trends in independent indices of abundance (catch per unit effort, night-light surveys) for California waters.

2. It is not necessary to assume an increase in rate of natural mortality from $M = 0.4$ to $M = 0.8$ in the 1950's to obtain reasonable biomass estimates.

3. A decrease in the relative abundance of 2- and 3-year-old fish occurred in the 1950's, possibly reflecting a progressively southerly origin of year classes. Failure to recognize this change caused a downward bias in previously published estimates of fishing mortality rates for the 1950's, wherein 3-year-old fish were assumed to be fully recruited.

4. The ratio of sardine spawning biomass to CalCOFI sardine larva census is double the previous value. A 95% confidence interval ranges from one-quarter to quadruple the estimated biomass. The relationship displays the expected statistical qualities, whereas the previously published relationship was artificially precise.

5. A purely functional description of the stock-recruitment relationship since 1932 shows no curvature (density-dependent regulation of recruitment), indicating little resilience to fishing. Had there been no fishing, the stock would, on the average, have done little better than replace itself. The average potential growth rate appears to have been 8.5%/year, with large fluctuations.

6. The apparently poor rates of recruitment in the 1960's are likely to be the result of including immigrant fish from the southern genetic group in estimates of spawning biomass of the northern stock. These southern fish may not be adapted to spawning in the relatively cool waters off California. Recruitment rates of the remaining fish from the northern genetic group may have been quite normal.

7. A simulation model of the sardine population containing "optimistic" biases showed the maximum continuous-fishing mortality rate that the sardine population could have sustained to have been $F = 0.25$ (22% annually).

8. The same model showed that the population could have sustained a constant annual quota of 300,000 metric tons but would have been seriously depleted by a 350,000 ton quota. Due to instability induced by a constant harvest from a fluctuating population, and to the "optimistic" bias of the model, maximum sustained yield for the northern stock was probably about 250,000 tons. This estimate is considerably lower than the previous estimate of 427,000 metric tons (Murphy 1966).

9. The Gulland potential yield estimation (Gulland 1970) would have estimated potential maximum sustained yield to be 640,000 metric tons, which would not have been sustainable. The Gulland estimator may have to be revised downward in the case of populations subject to large natural fluctuations in abundance.

ACKNOWLEDGMENTS

I wish to thank Joe Caruso and Steve Reilly for their help in checking the computations and Kate Coleman for typing the manuscript.

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SEA SURFACE TEMPERATURE ANOMALIES

Douglas R. McLain¹

Monthly mean sea surface temperatures and their anomalies, or departures from a 20-yr (1948-67) mean, for 1976 have been mapped for the Gulf of Alaska-Bering Sea, the eastern North Pacific, and the western North Atlantic (Appendix 9.1). The western North Atlantic was mapped for 1974 (McLain 1976) and all three areas were mapped for 1975 (McLain 1978). The maps are based on surface marine weather observations made routinely by ships of many nations.² The observations are available in near real-time and at low cost, and are used to produce several data products including these monthly mean maps. There are other maps of sea surface temperature available, in particular gulfstream³ and Fishing Information.⁴ The areas covered are distinct and there are a few important processing differences. Fishing Information uses the same 20-yr base period as the present maps. The temperatures and anomalies are contoured and thus reflect analysis; the data are not presented. The gulfstream presents the data and uses a full data set historical mean. The reference period includes years of sparse data, particularly before World War II, and clusters of data from classical research cruises.

Technique

The observations of sea surface temperature were edited through a two-stage filter. In the first stage, all observations <-2.00 or >4.00 were rejected. In the second stage, observations >8.00 from a reference value were rejected. The reference value was the base period mean for the particular month and the particular

¹Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93940.

²The marine weather observations are transmitted worldwide over the GTS network. They are received at the Fleet Numerical Weather Central, U.S. Navy, Monterey, CA 93940.

³The gulfstream, Oceanographic Services Branch, National Weather Service, NOAA, Silver Spring, MD 20910.

⁴Fishing Information, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

1-deg square for the first two observations of that month; for later observations the reference value was the current mean for the particular month and 1-deg square.

Saur (1963) and McLain (1976, 1978) discussed sources of error in the observations and in the maps.

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SAUR, J. F. T.

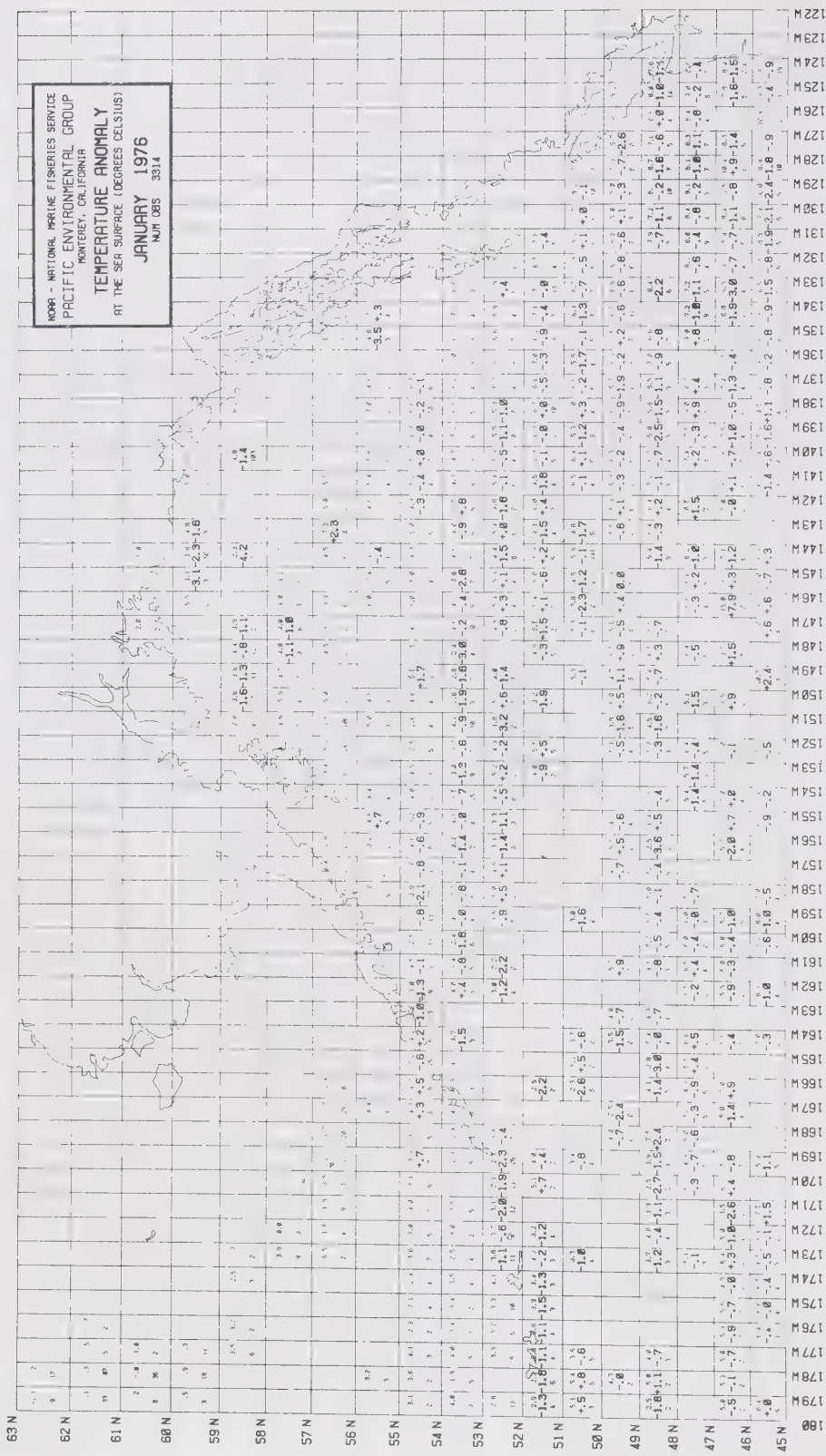
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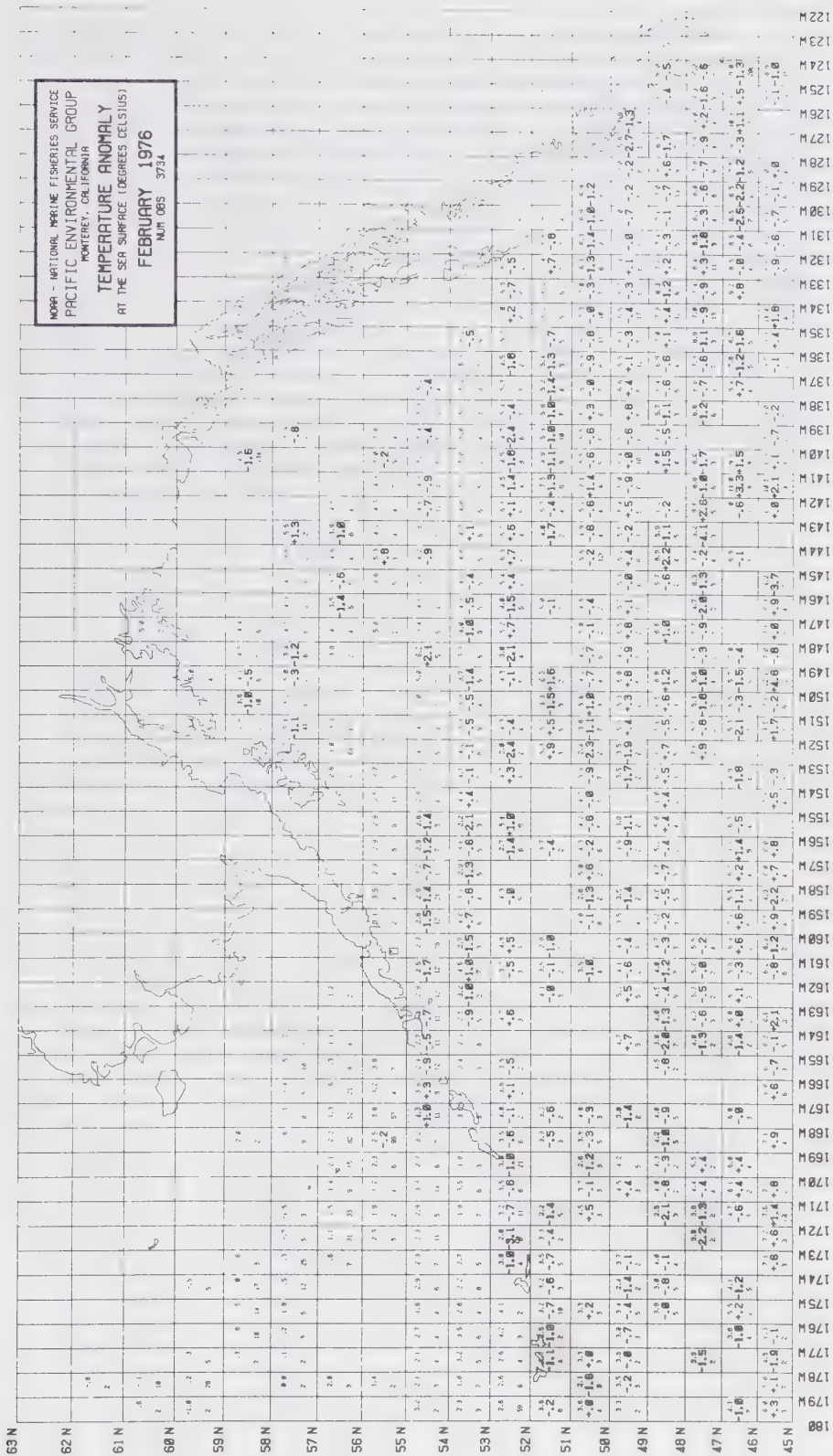
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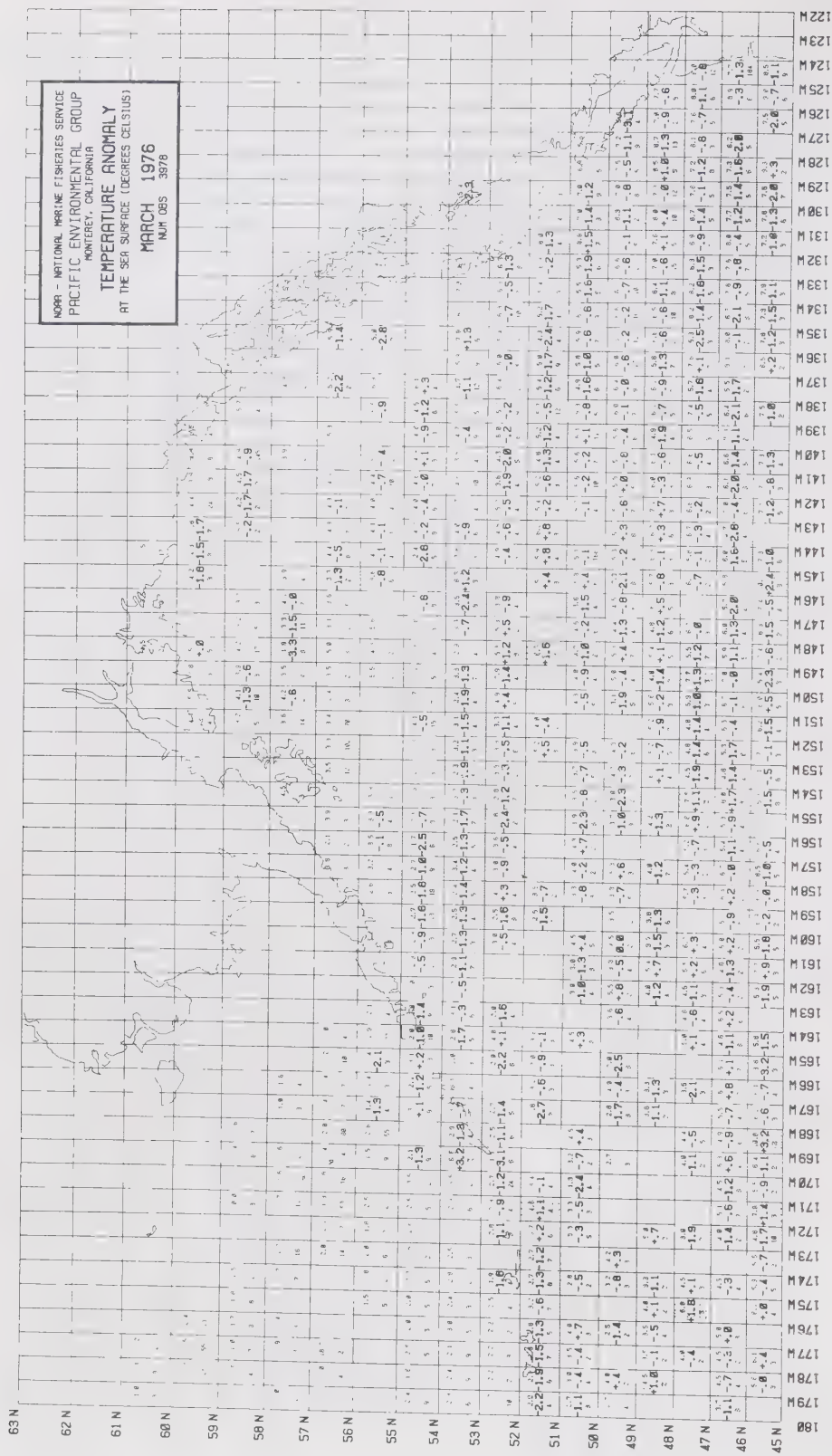
The maps present by month and by 1-deg square the mean monthly sea surface temperature, the departure from a 20-yr (1948-67) mean, and the number of accepted observations. The temperatures were not plotted if there were two or fewer observations in that particular 1-deg square. Also, anomalies were not plotted if there were fewer than five years represented in the 20-yr mean. Anomalies of magnitude greater than 1.0C are shaded.

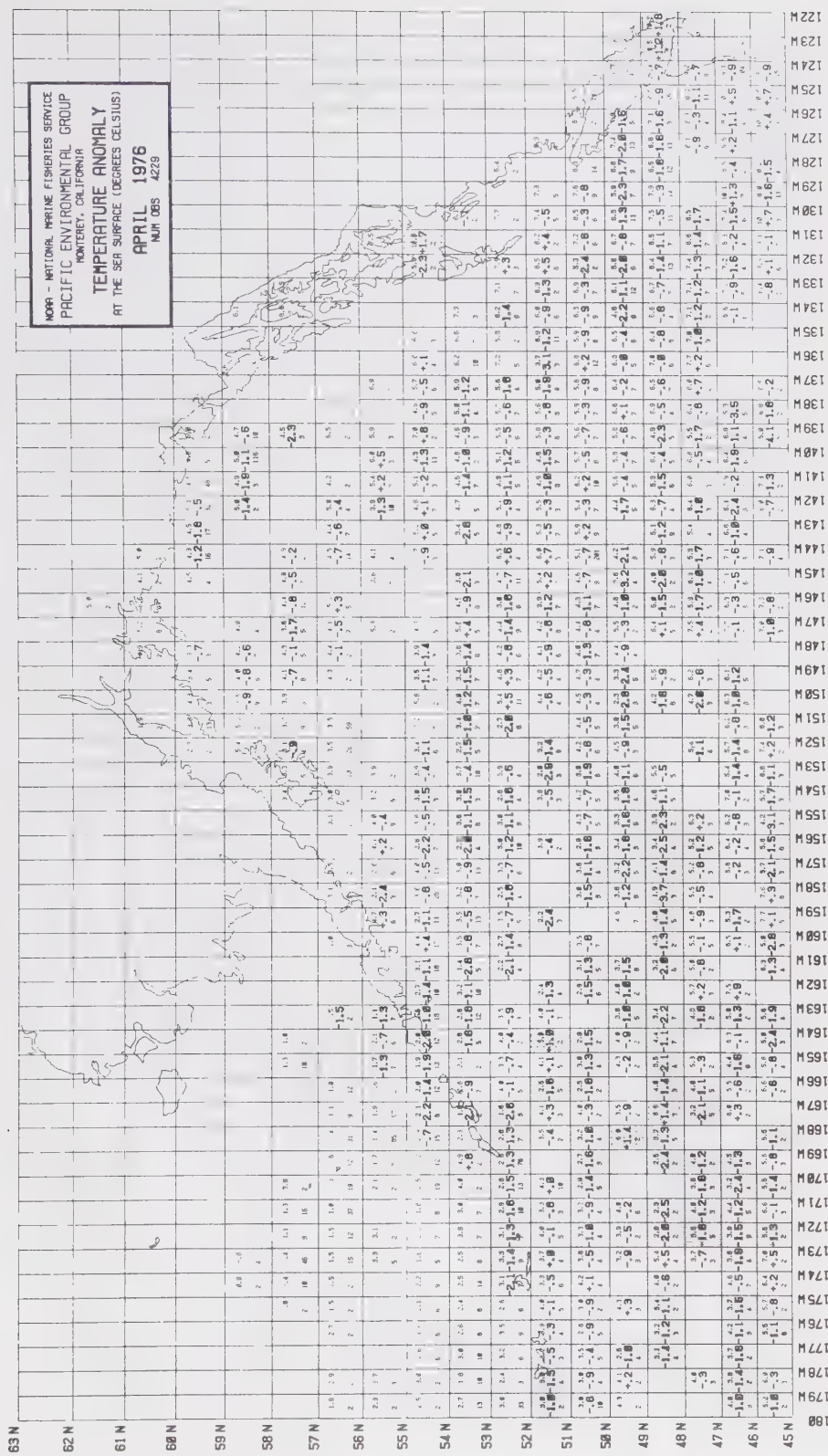
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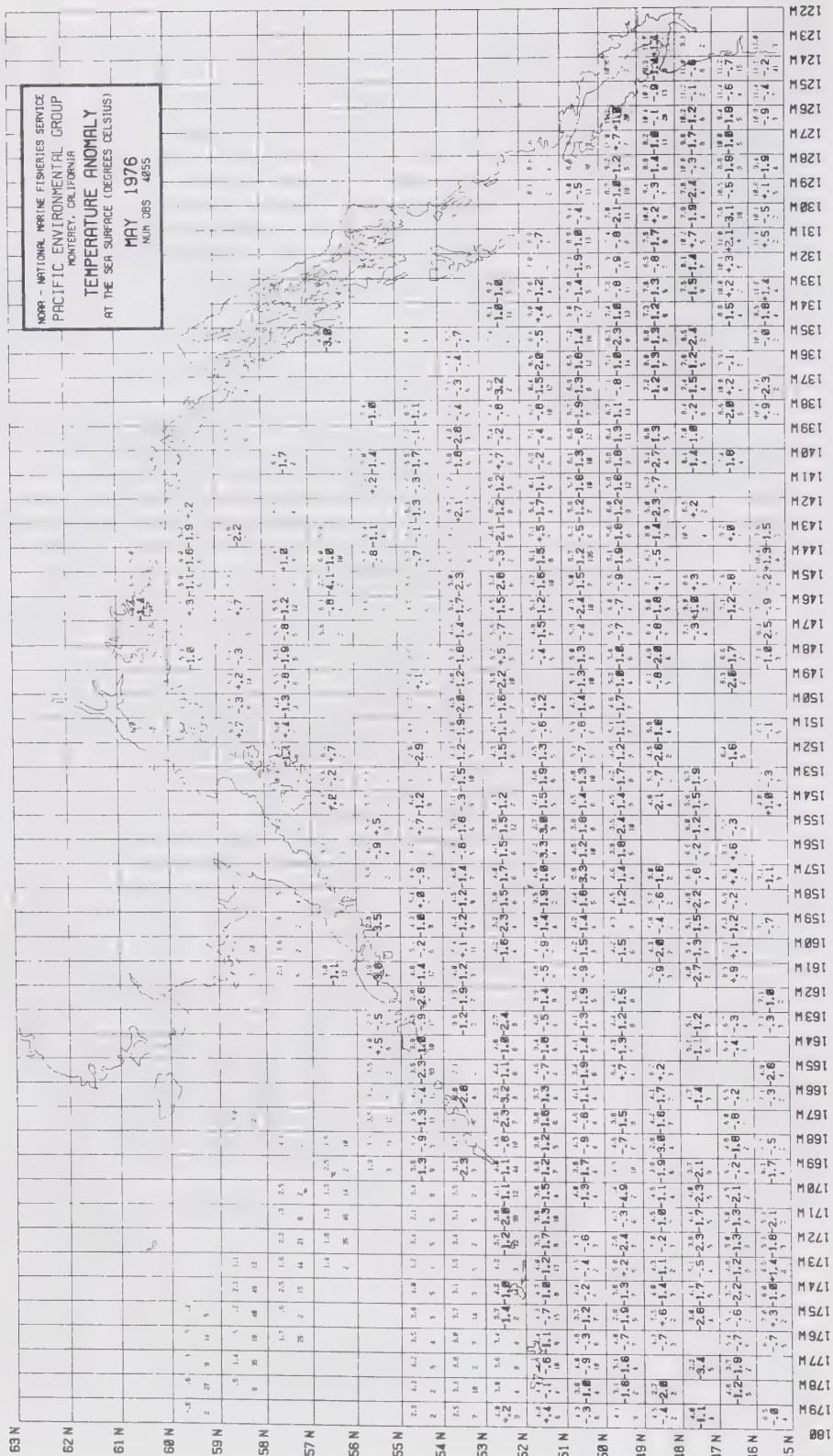
Gulf of Alaska and Bering Sea	45N-63N	122W-180W
Eastern North Pacific	25N-50N	110W-150W
Western North Atlantic	20N-46N	60W- 99W







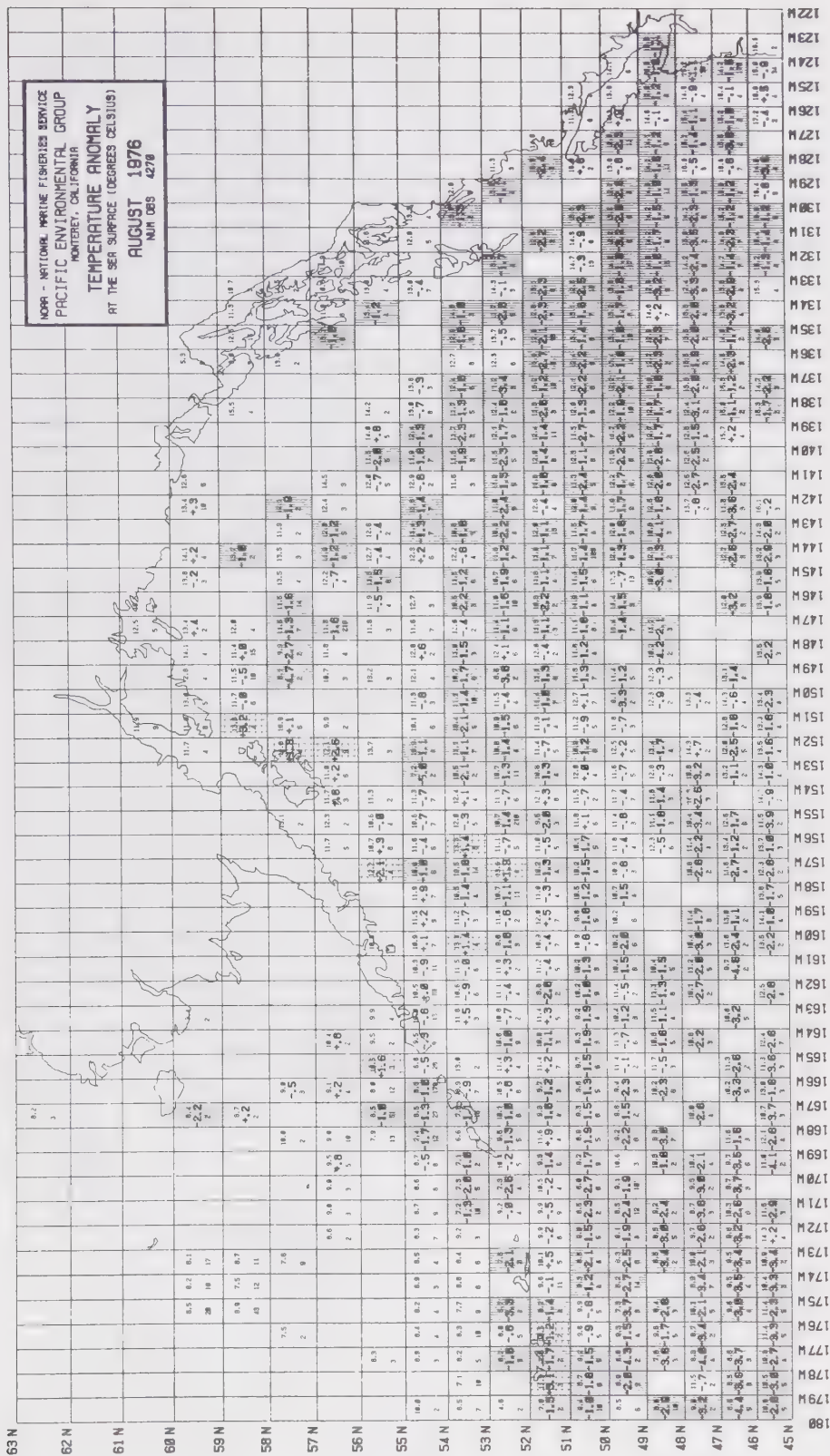


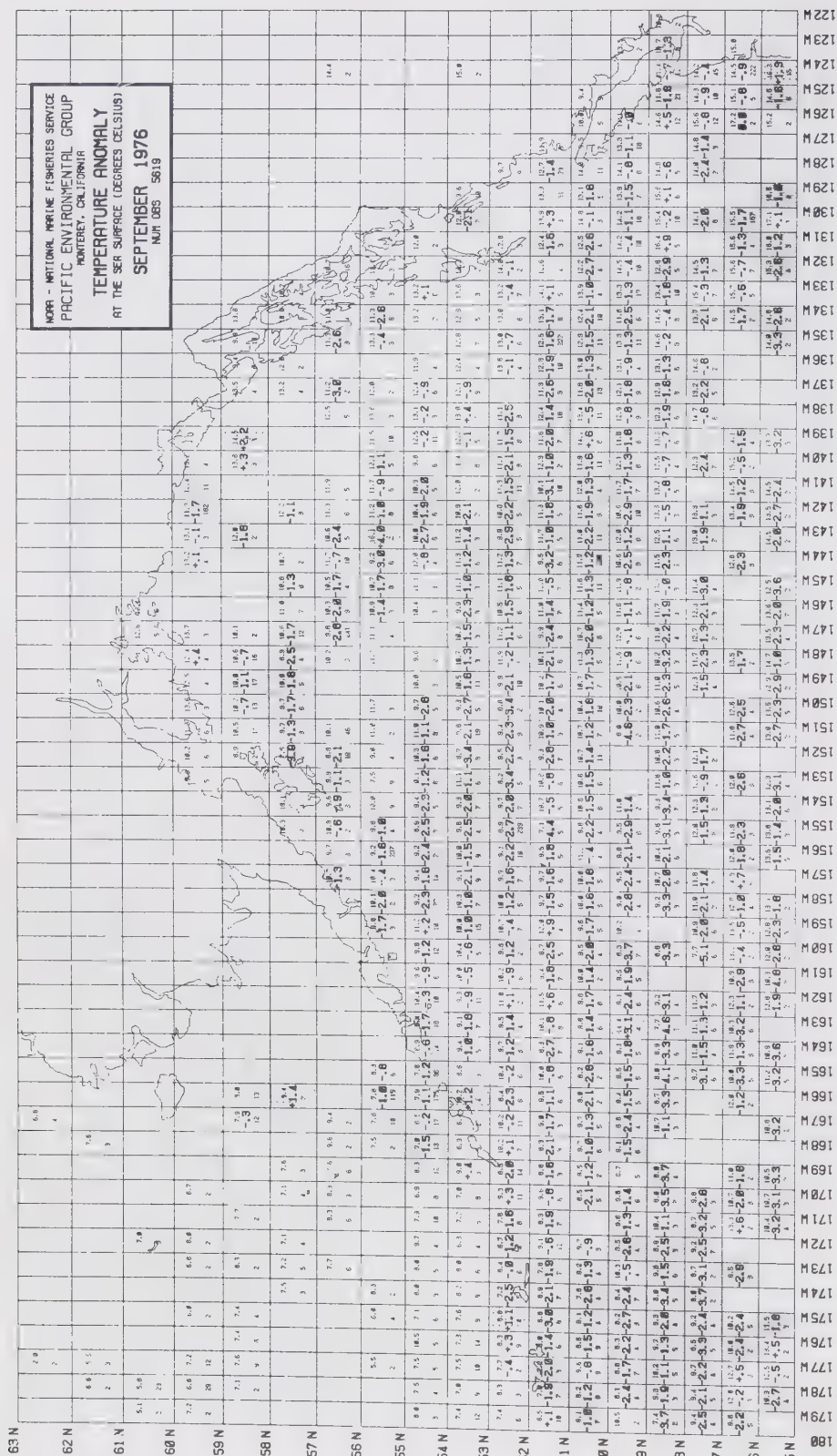


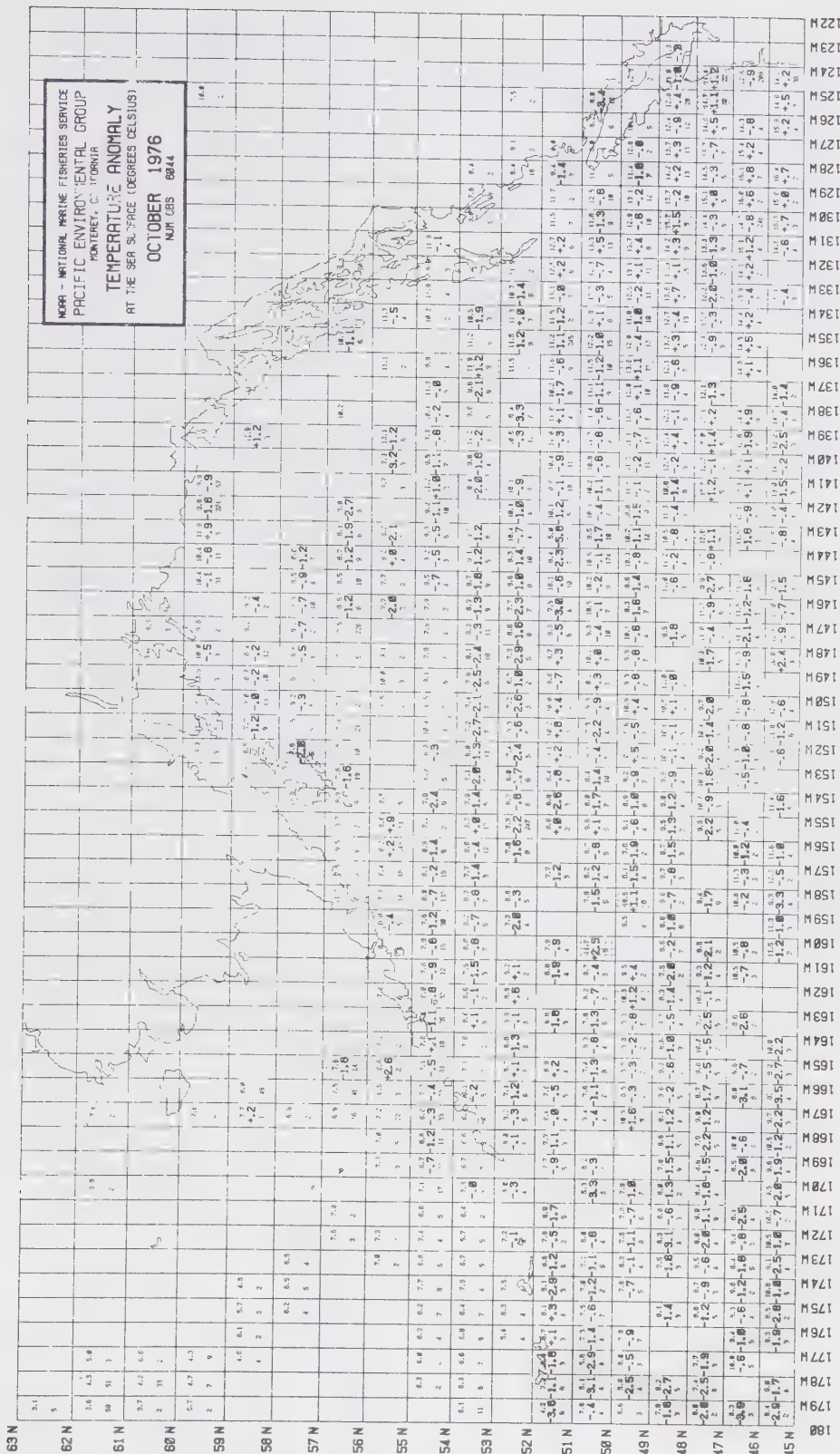


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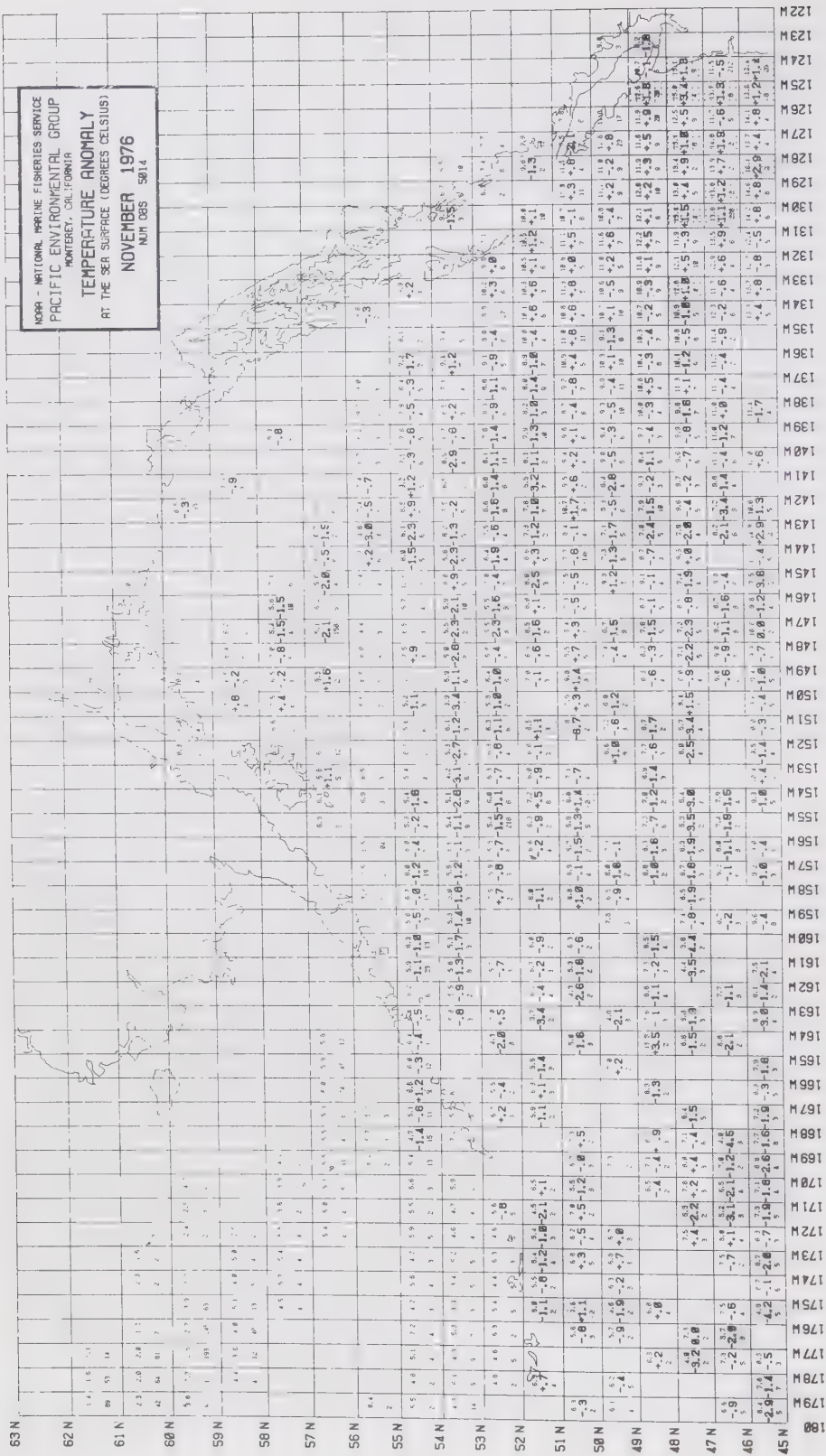


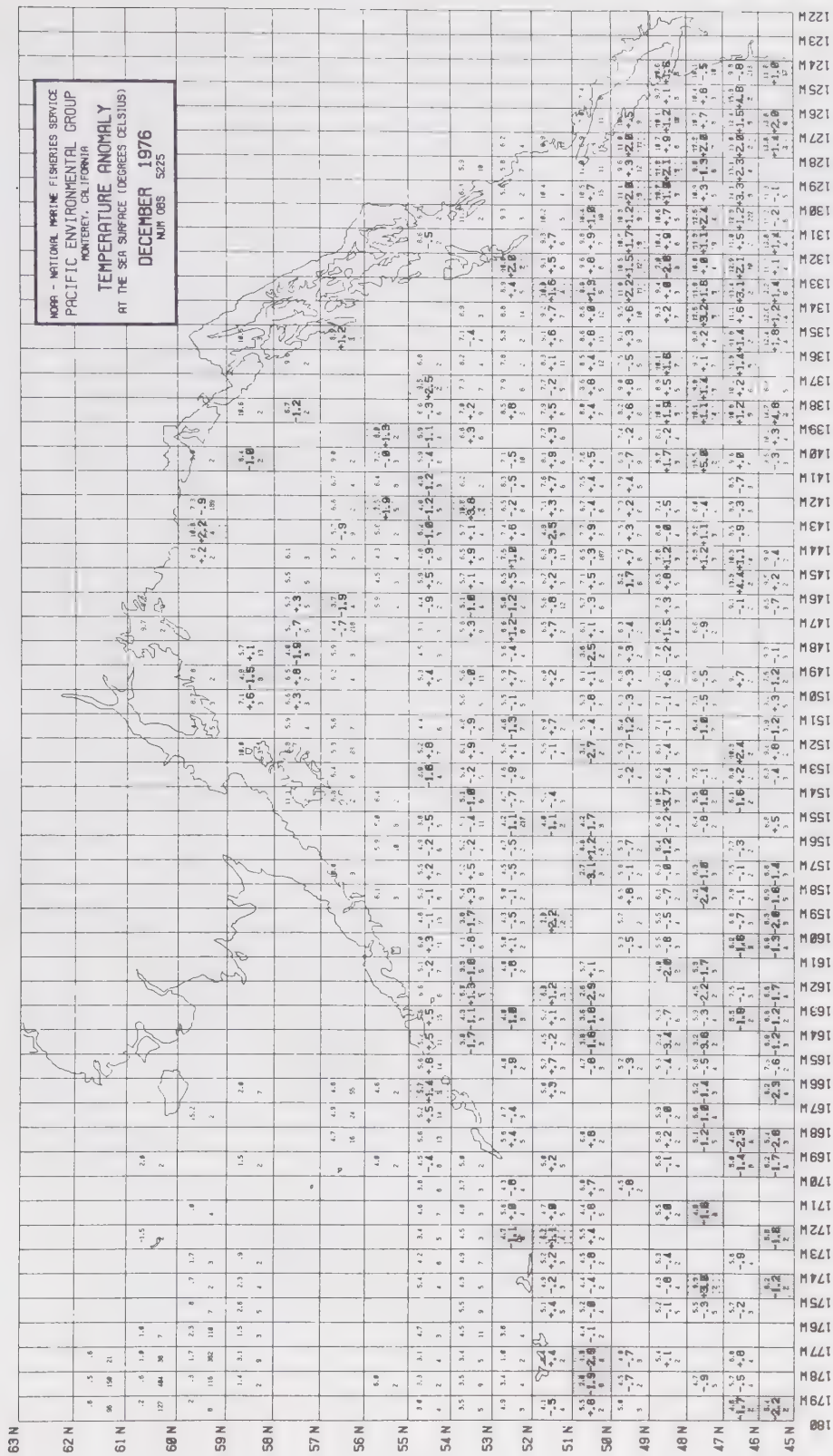






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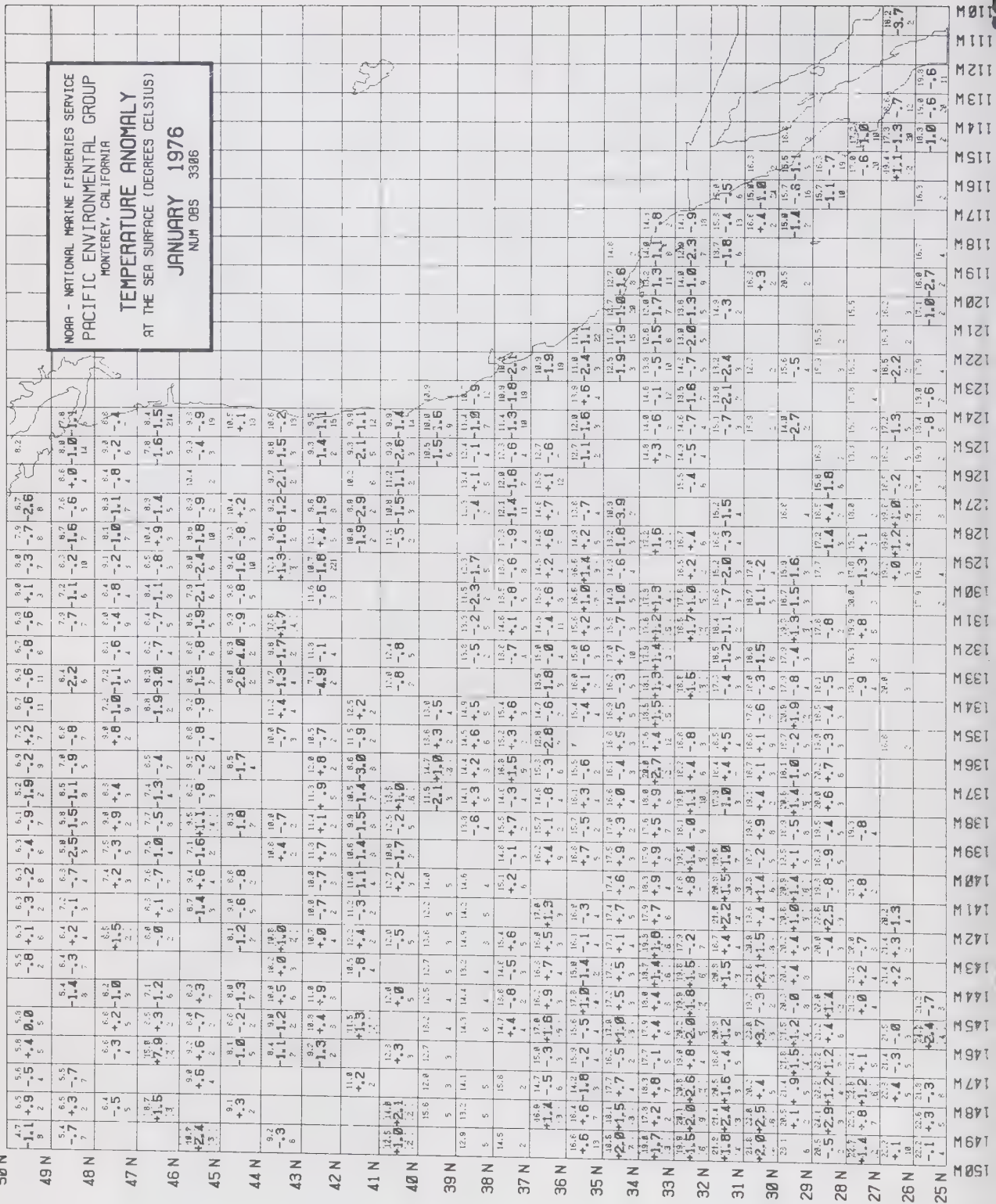




NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA

TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)

JANUARY 1976
NUM OBS 3306



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PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)

FEBRUARY 1976
NUM OBS 3235



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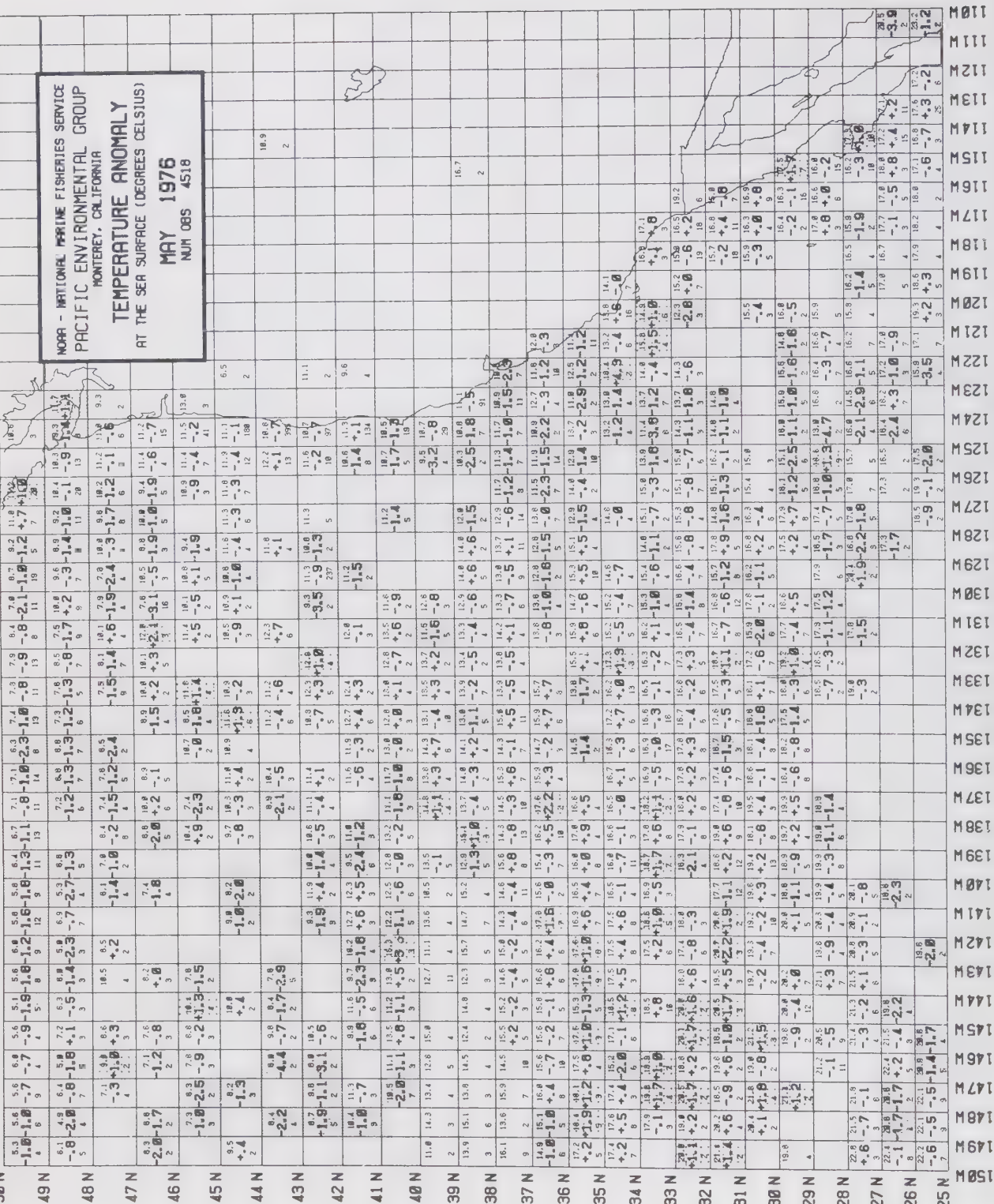
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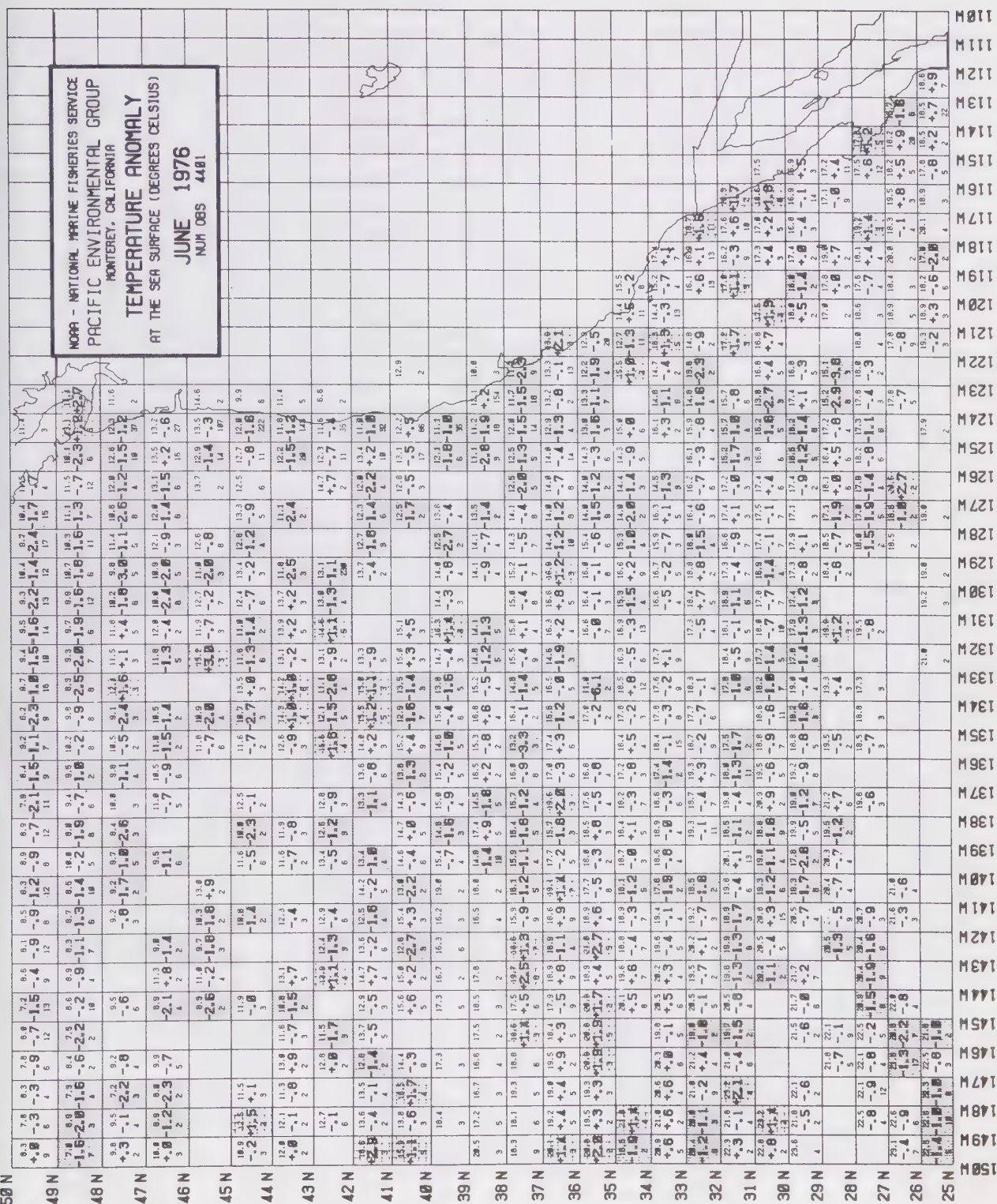
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PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)
MAY 1976
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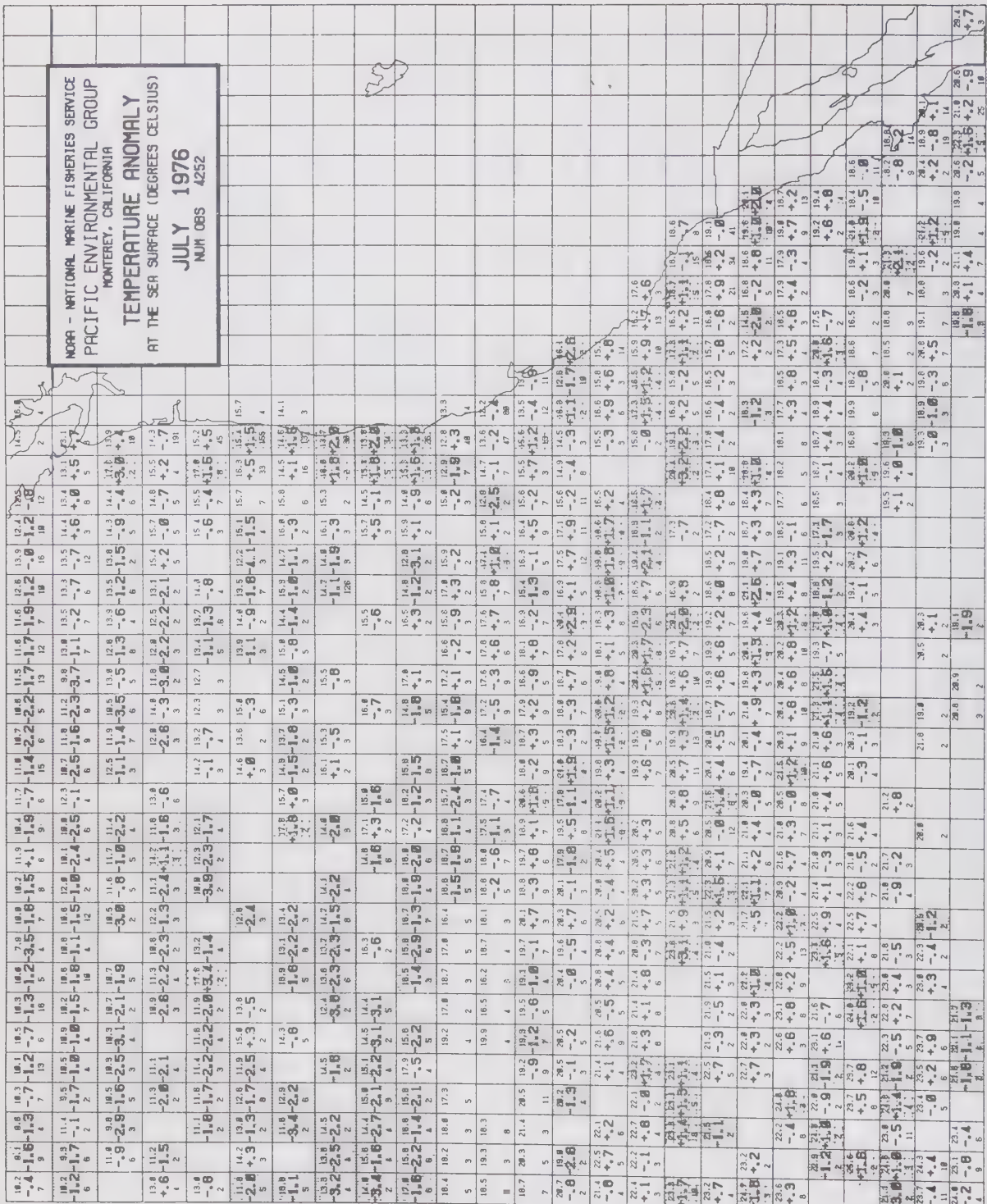
NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)

JUNE 1976
NUM OBS 4481



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PACIFIC ENVIRONMENTAL GROUP
MONTREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)
JULY 1976
NUM OBS 4252



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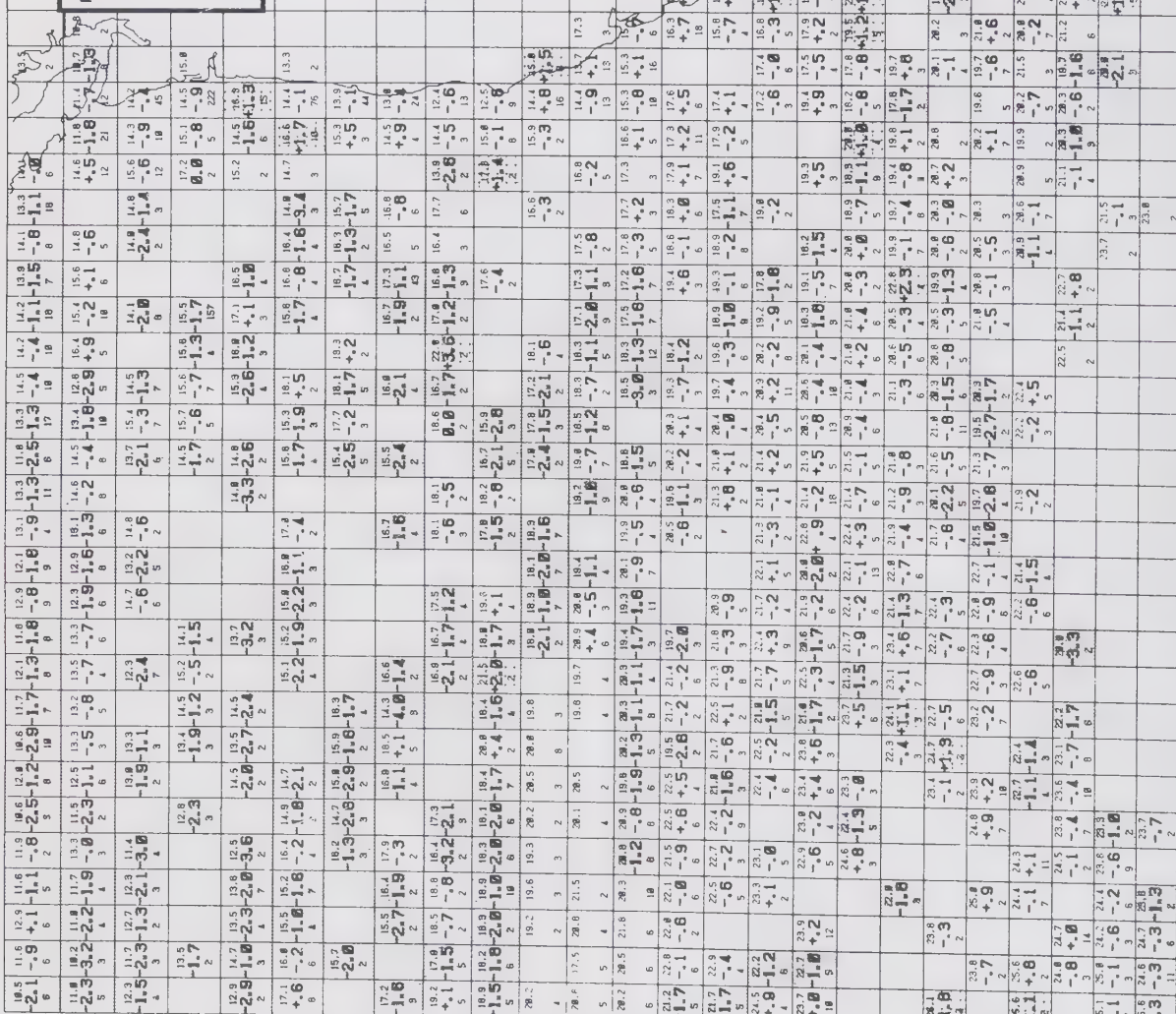
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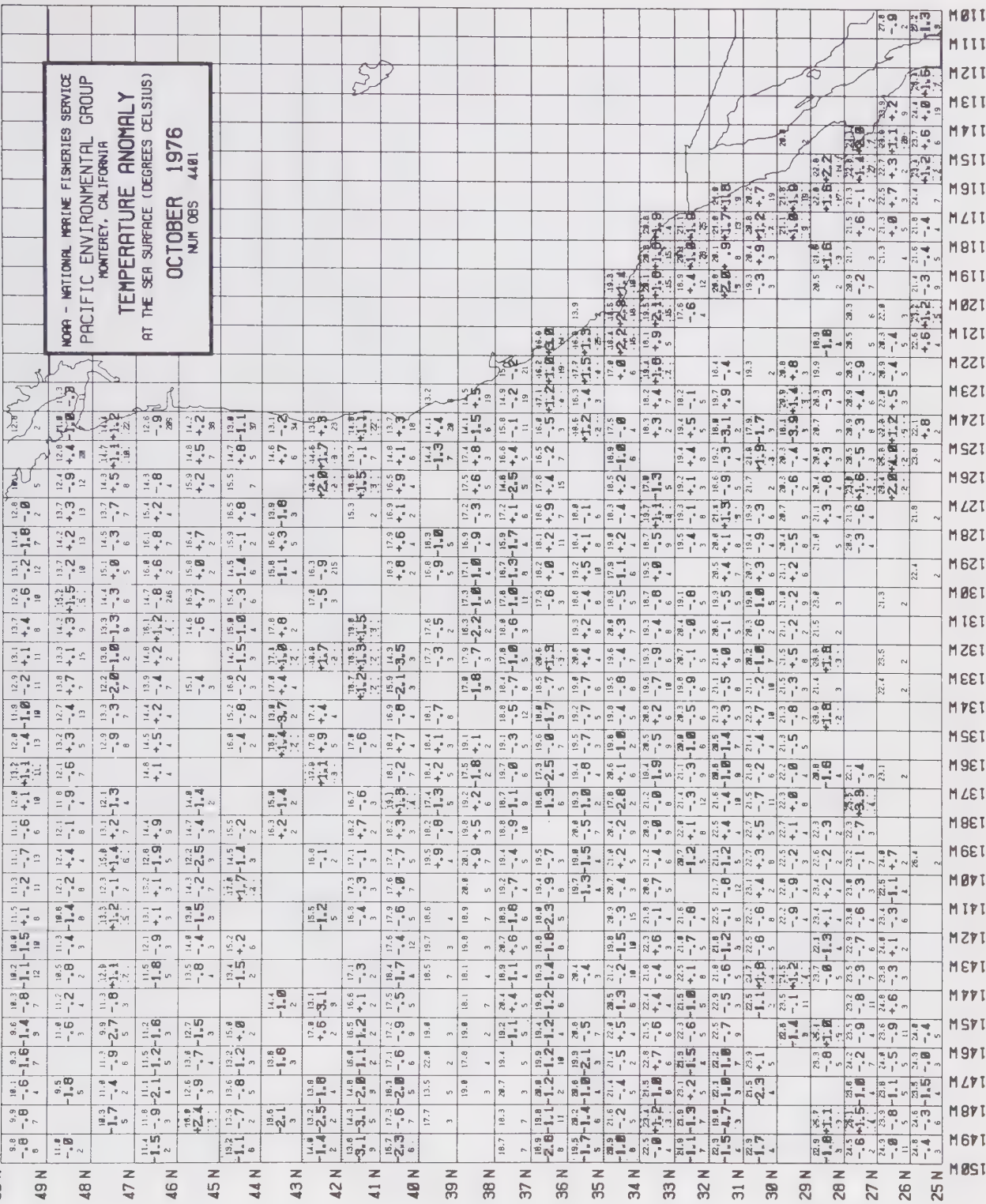
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NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)
SEPTEMBER 1976
NUM OBS 3493



50N



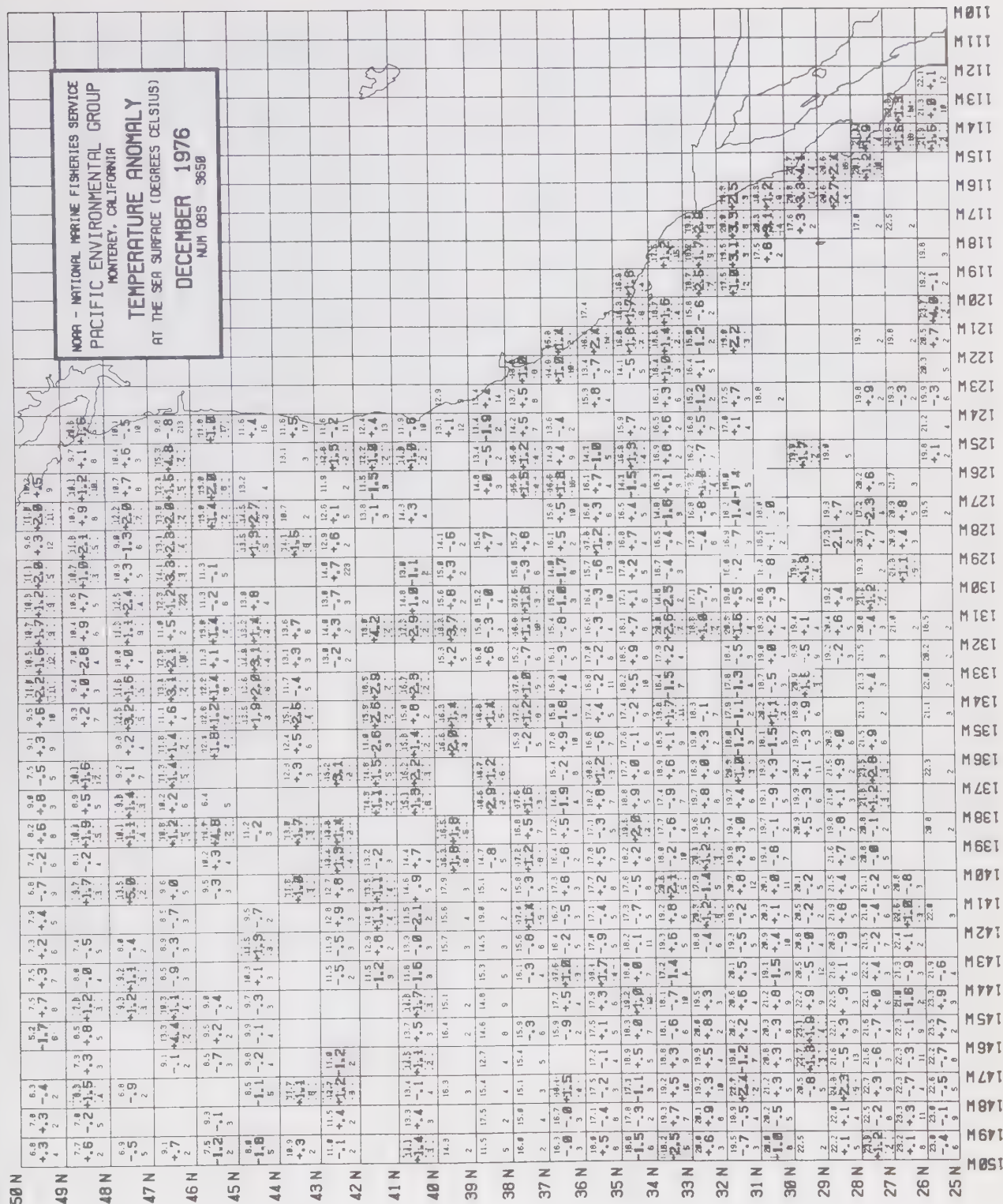
NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA

TEMPERATURE ANOMALY

AT THE SEA SURFACE (DEGREES CELSIUS)

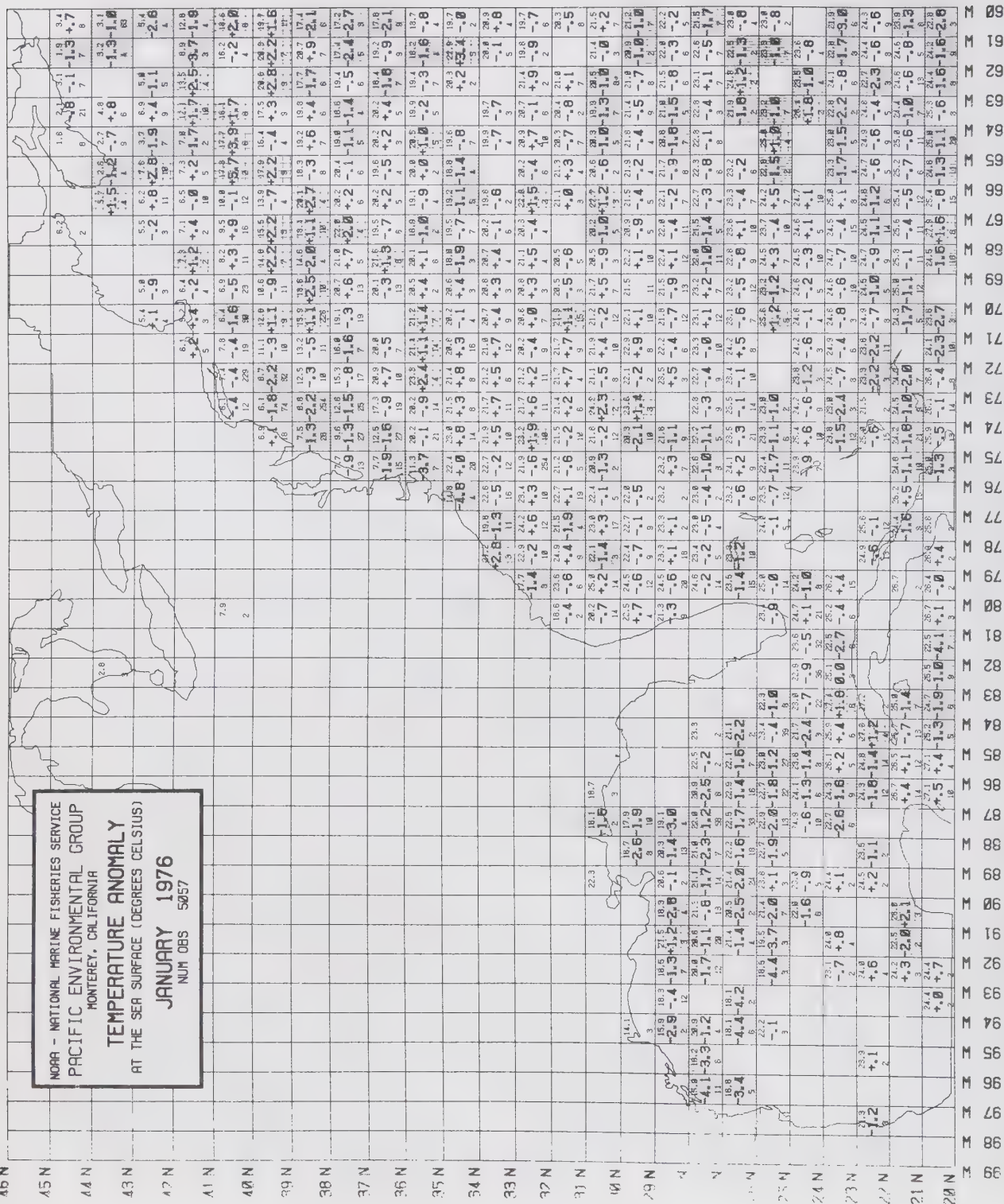
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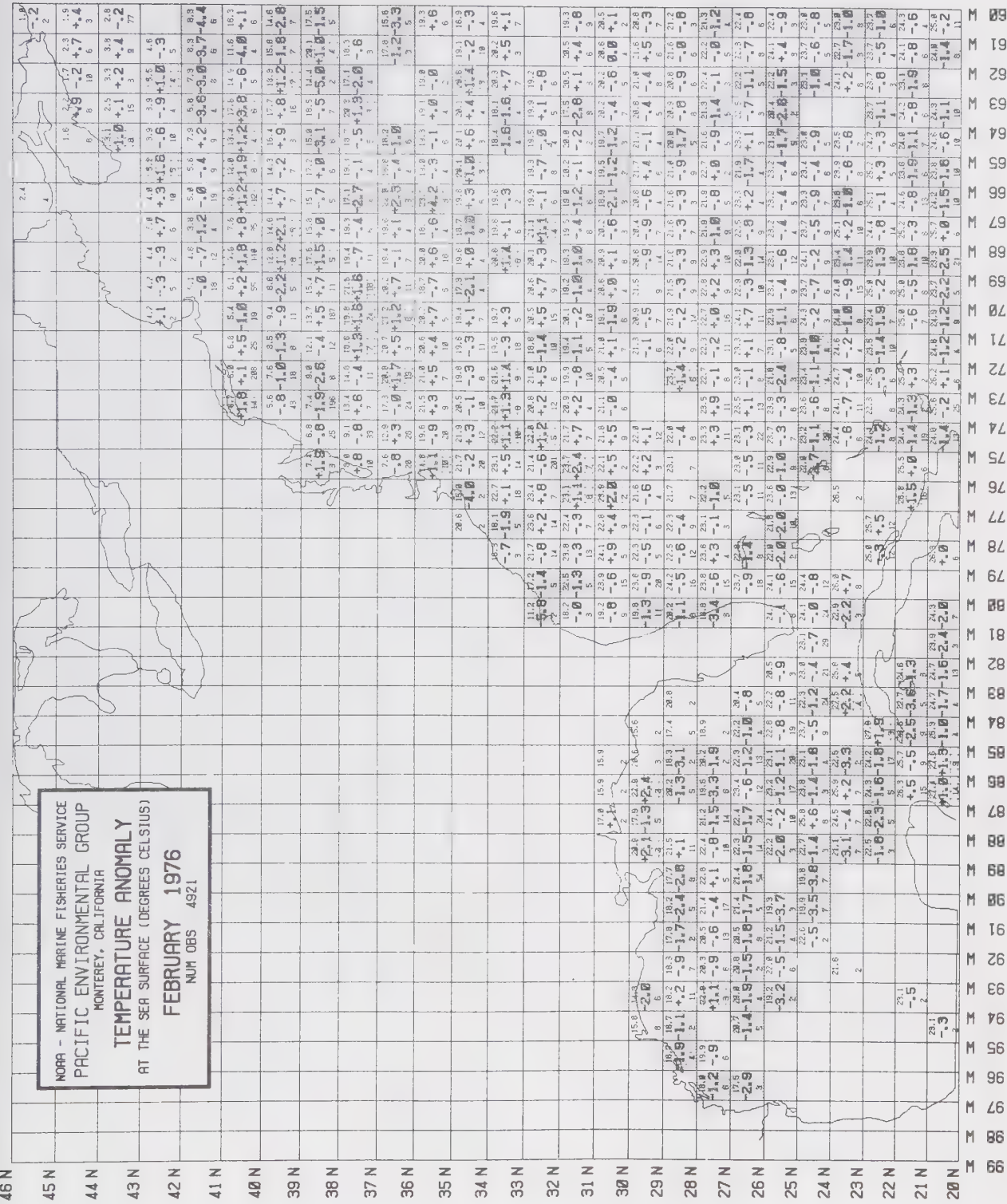


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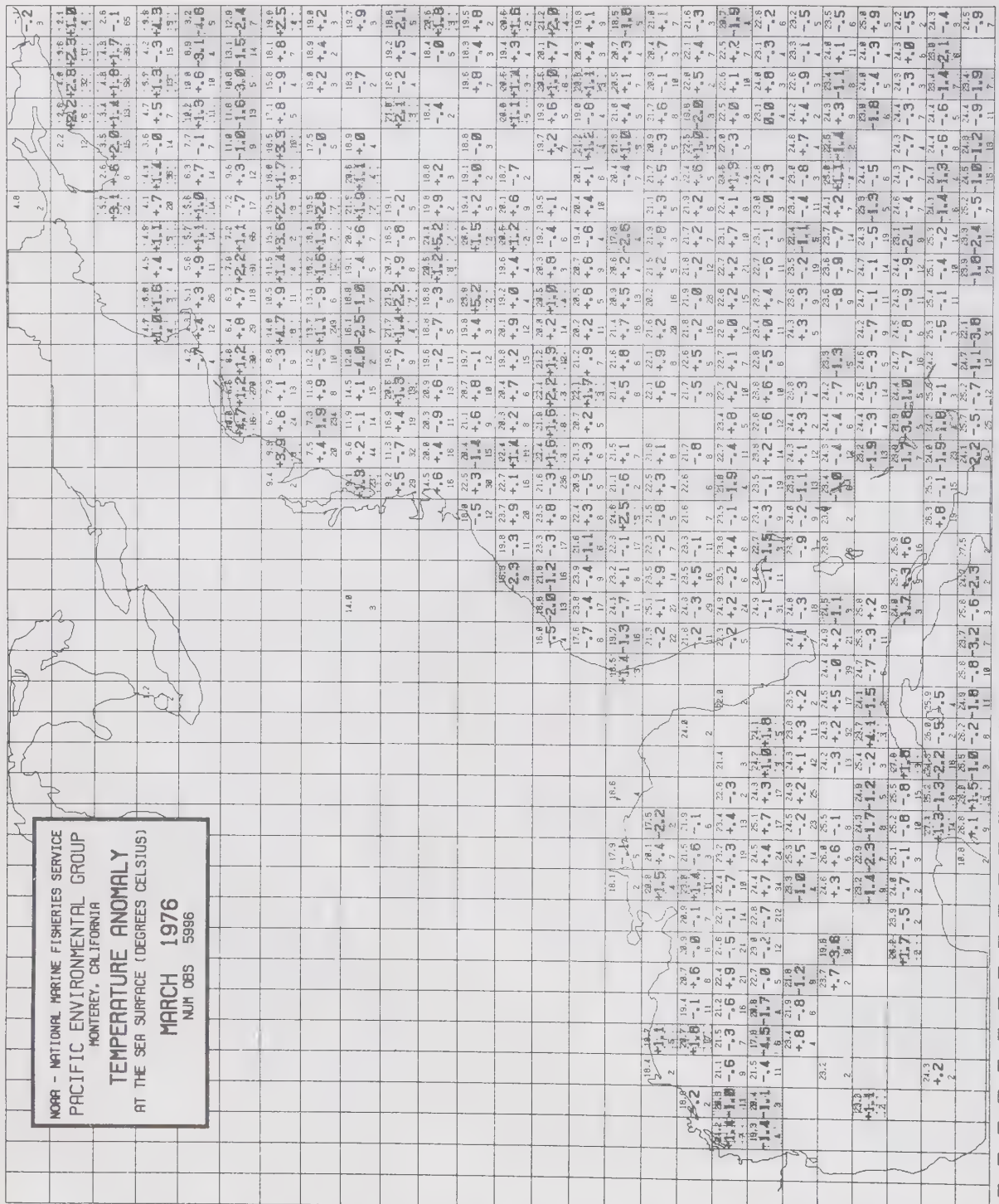


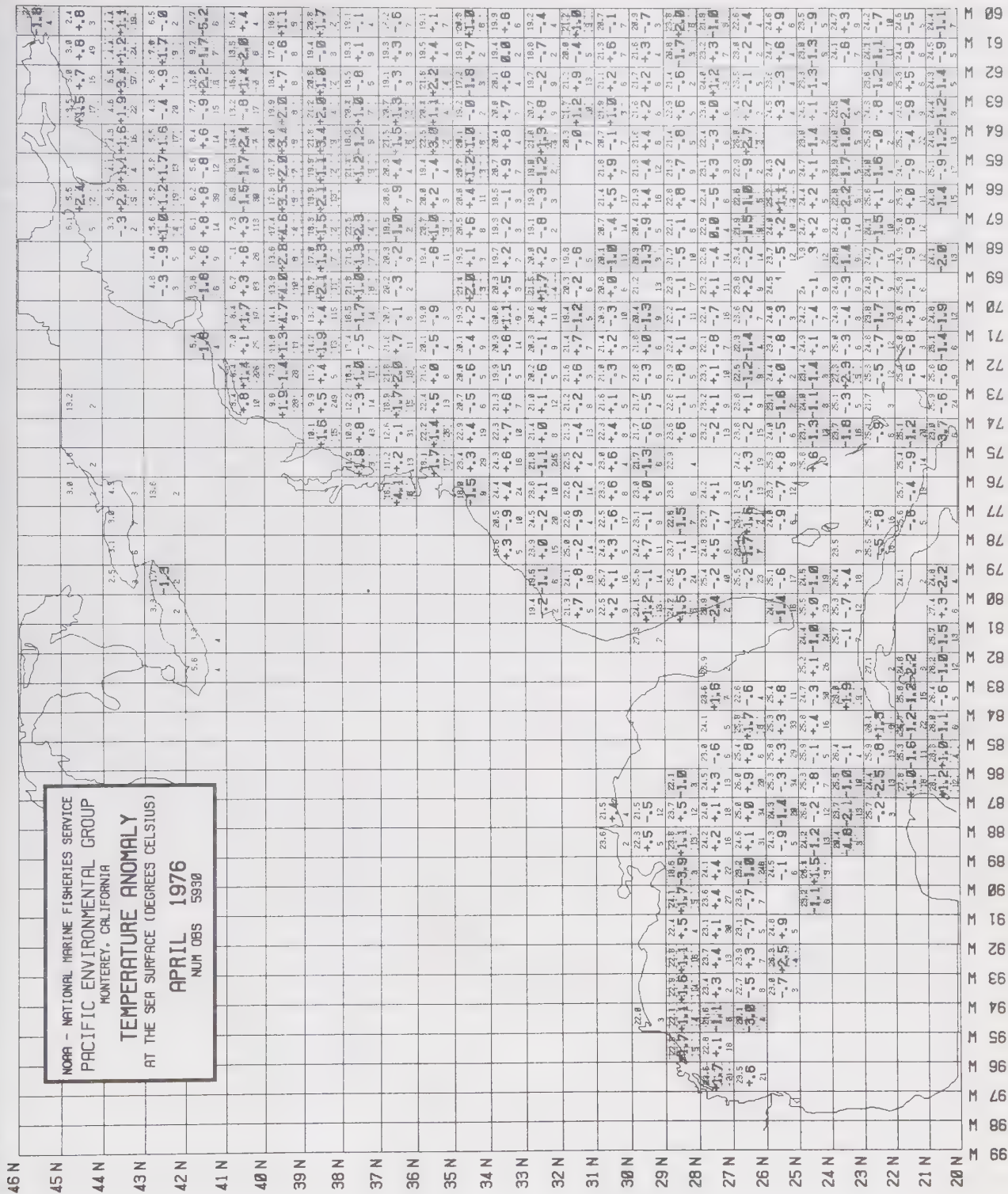
NORR - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEABOARD (DEGREES CELSIUS)
FEBRUARY 1976
NUM OBS 4921



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NORR - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)
MARCH 1976
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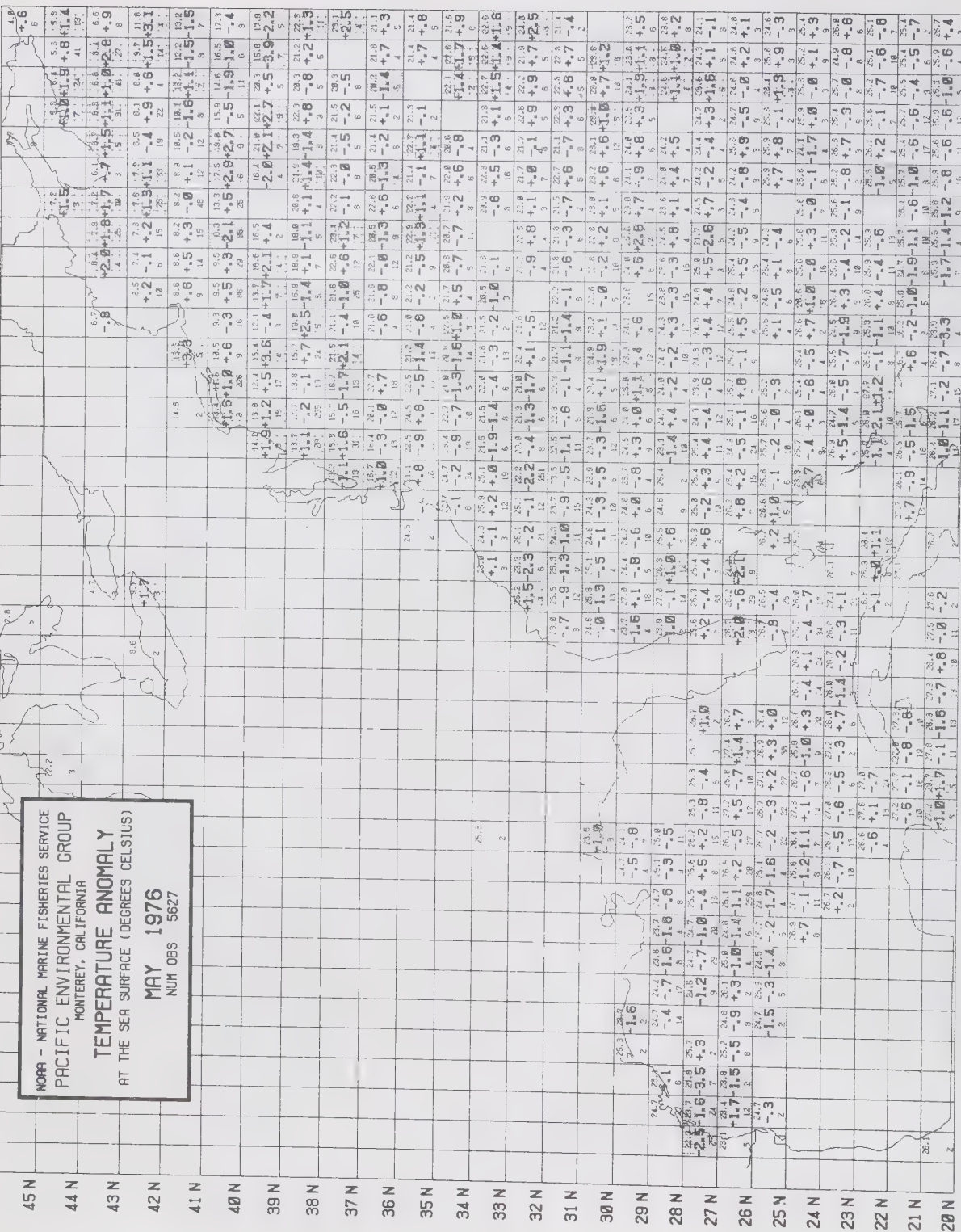


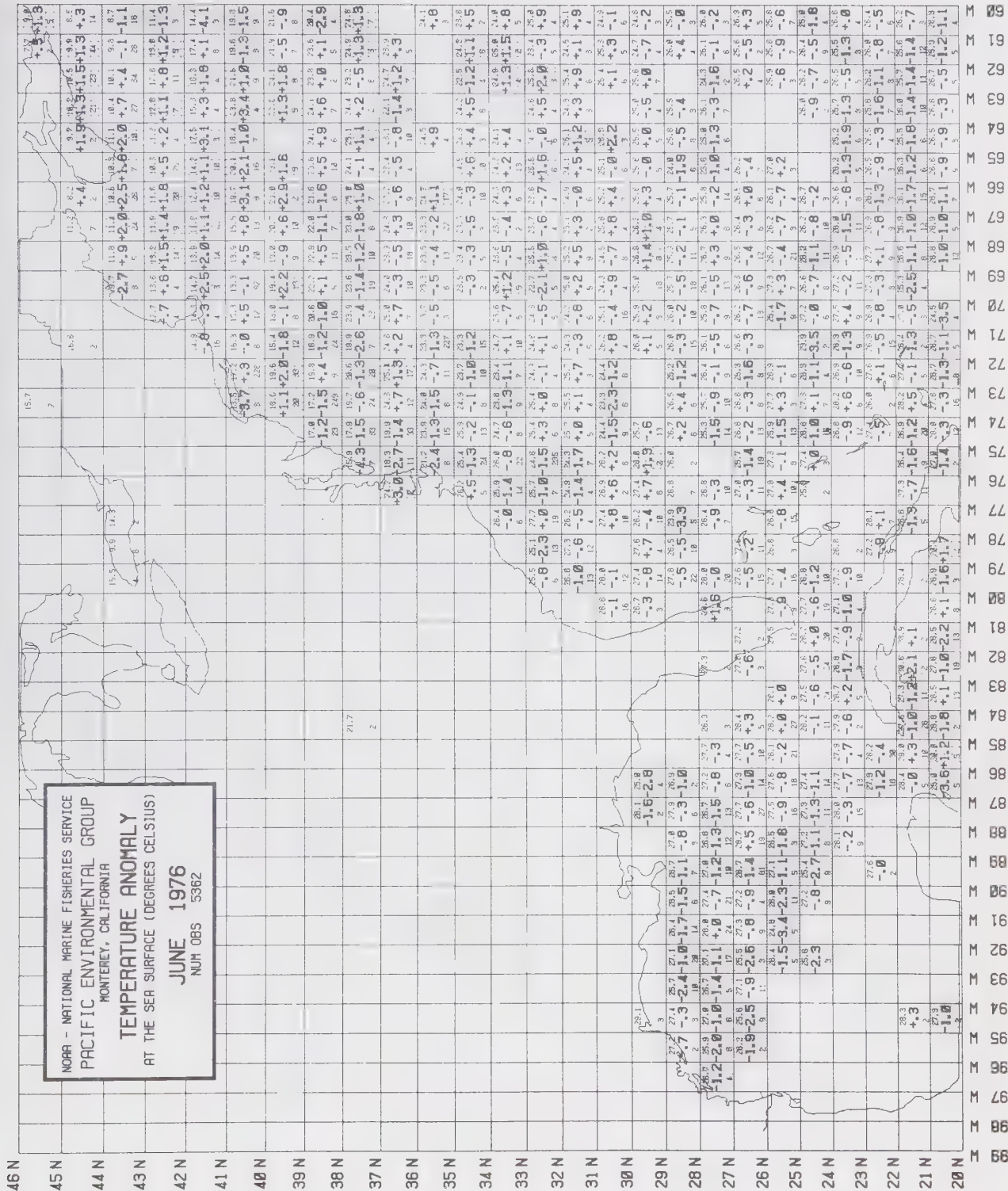


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NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)

MAY 1976
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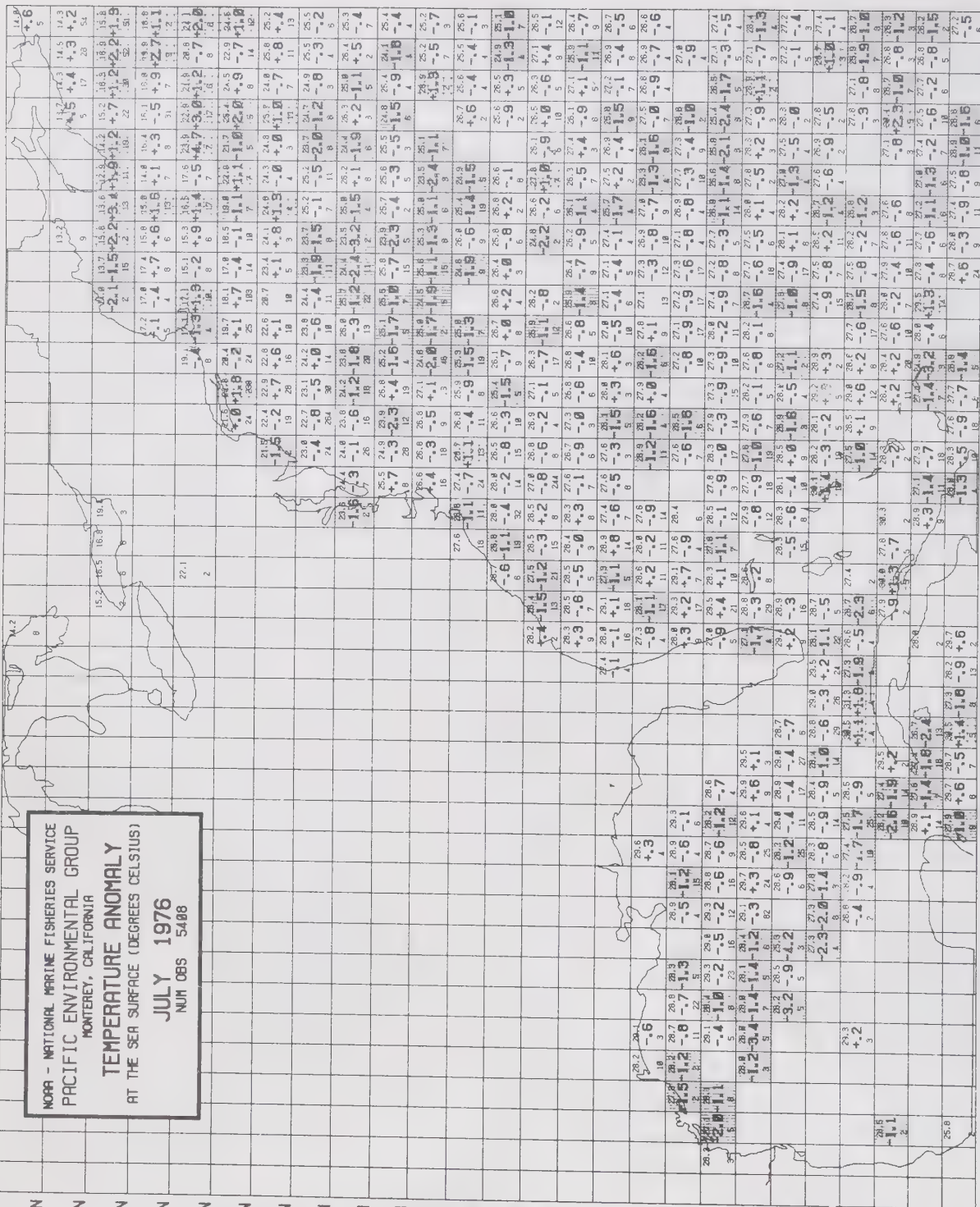




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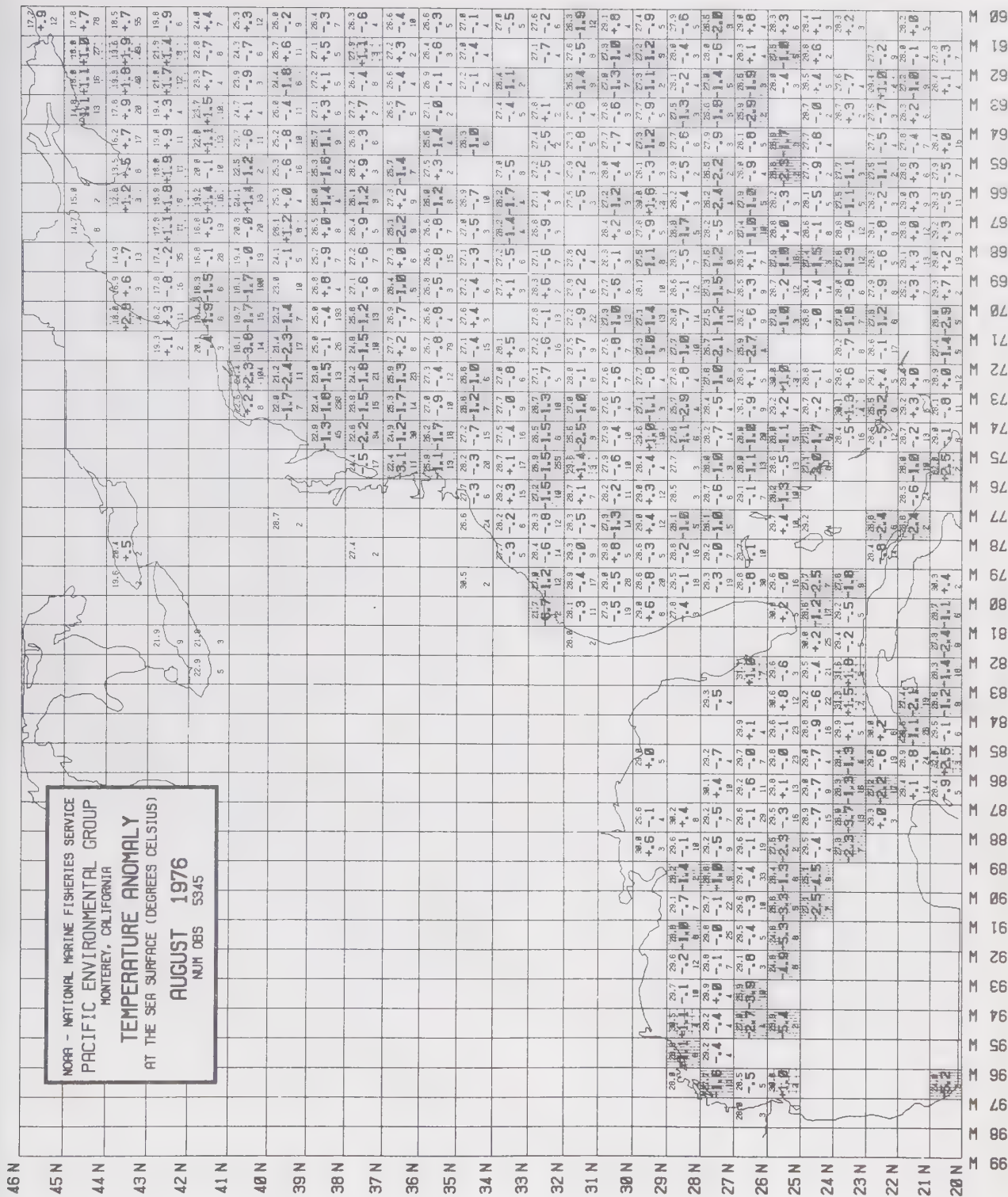
NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)

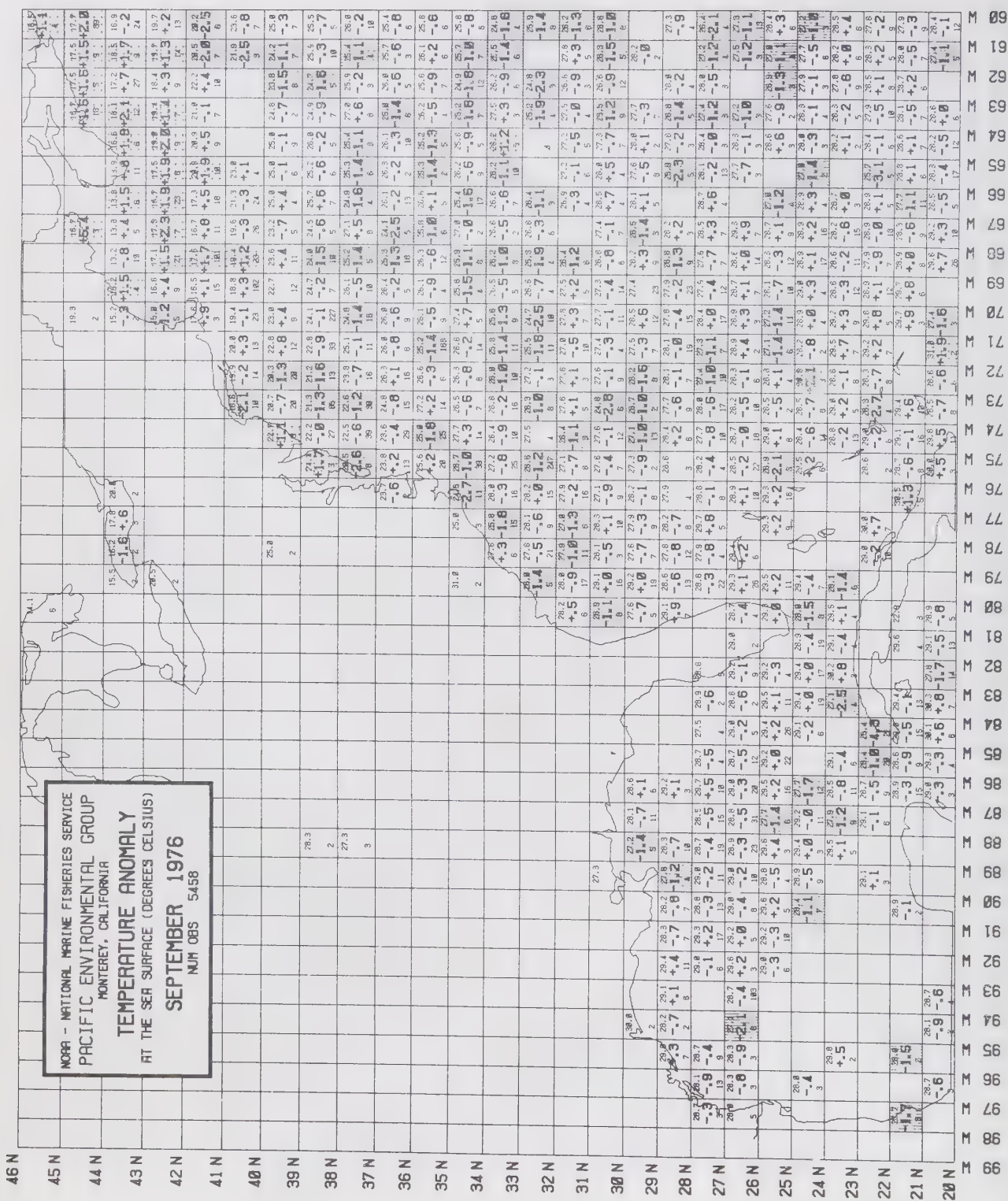
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NUM OBS 5488



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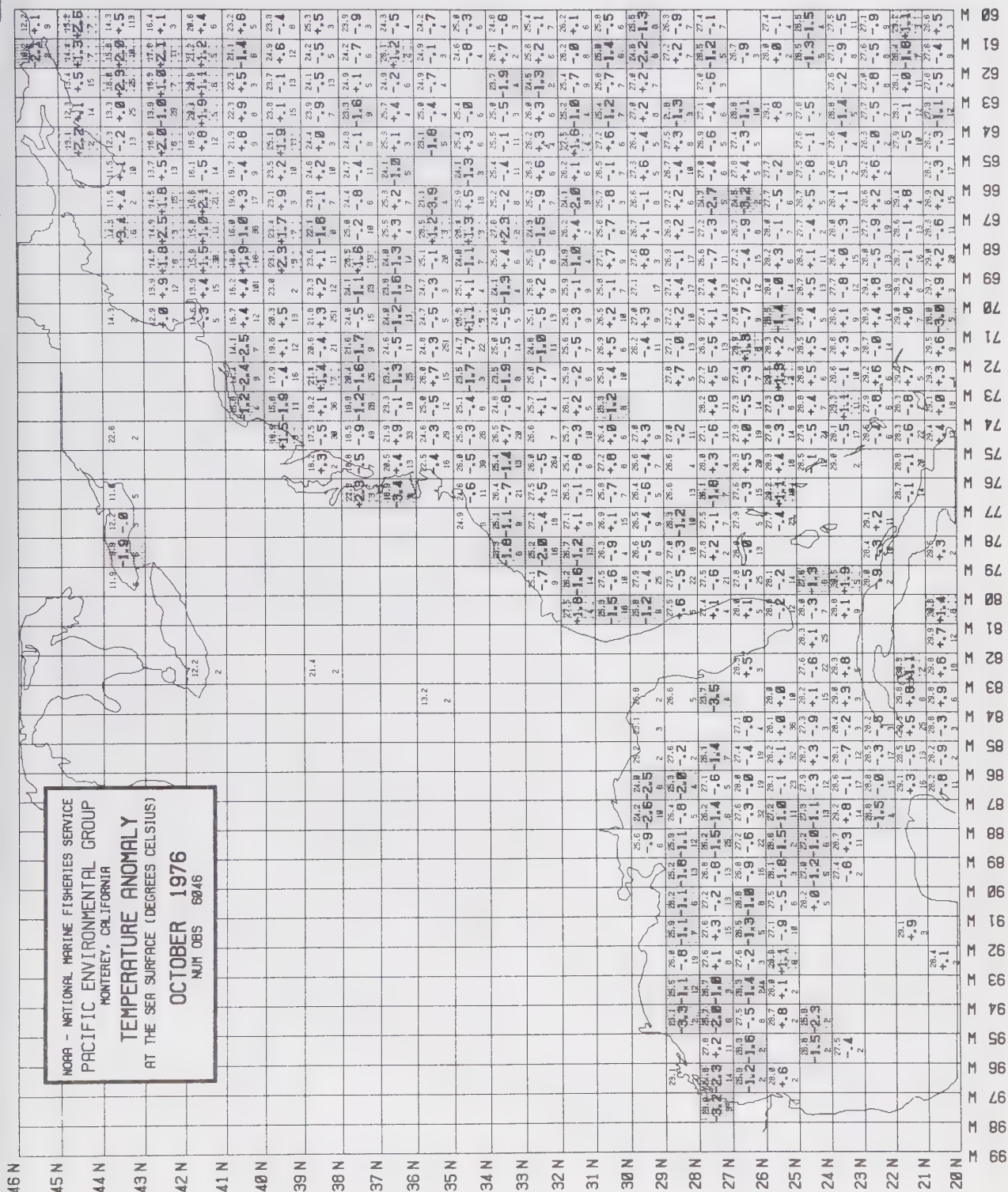
NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)
AUGUST 1976
NUM OBS 5345





NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)

OCTOBER 1976
NUM OBS 5046



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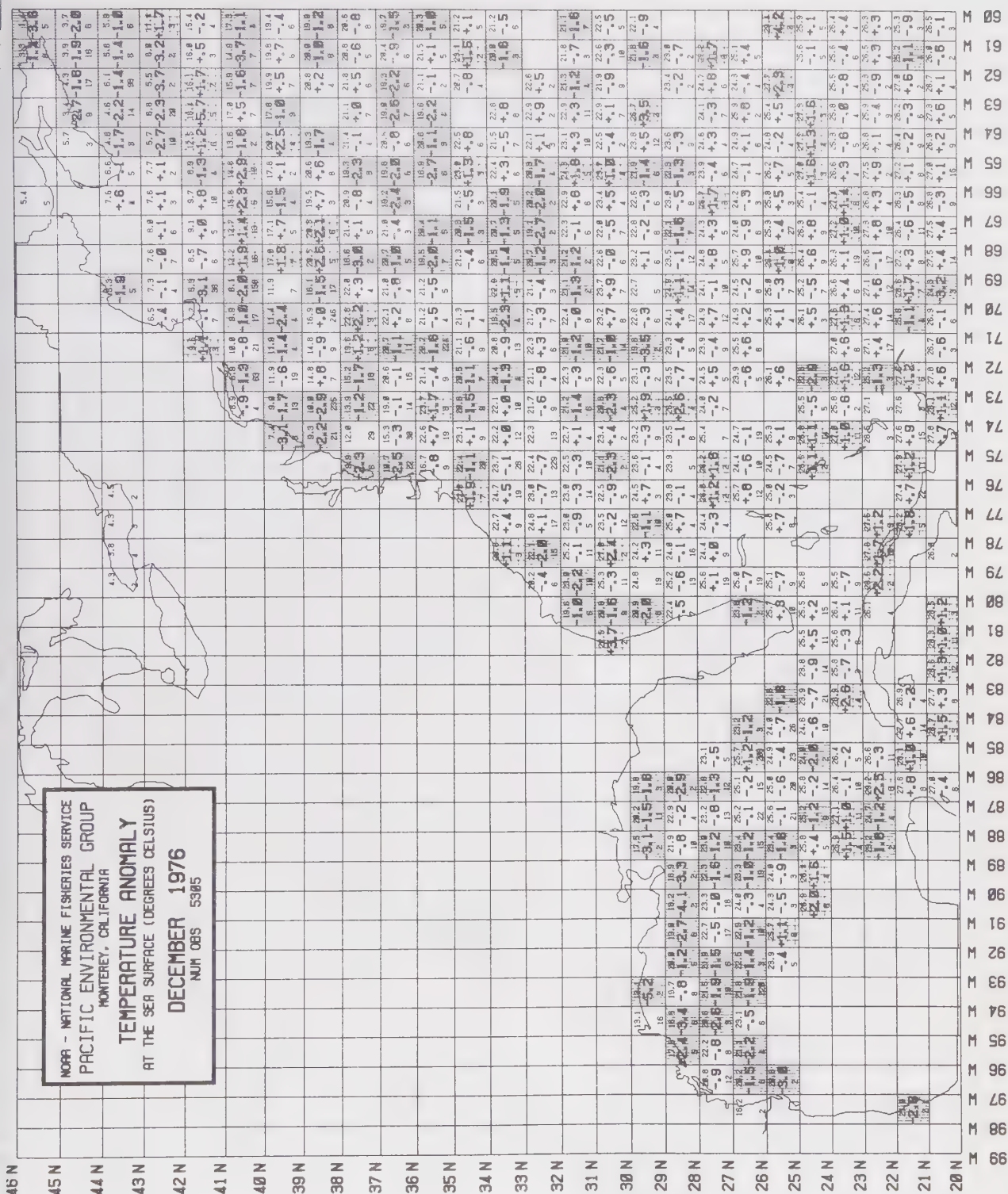
NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)
NOVEMBER 1976
NUM OBS 5382

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NOAA - NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
TEMPERATURE ANOMALY
AT THE SEA SURFACE (DEGREES CELSIUS)

DECEMBER 1976

NUM OBS 5385



FLUCTUATIONS OF SEA SURFACE TEMPERATURE AND
DENSITY AT COASTAL STATIONS DURING 1976

Douglas R. McLain¹

Sea surface temperature (SST) and density measurements have been made routinely at many U.S. National Ocean Survey (NOS) tide gages and other coastal stations for many years. Although the data suffer from various problems such as gaps in coverage or inadequate exposure to open ocean conditions, careful selection of stations allows the data to be used as an inexpensive monitor of climatic fluctuations in nearshore waters. This report summarizes monthly mean SST and density fluctuations for 1976 and long-term means for three coasts of North America. The data are contoured in a common manner for each coast to flag unusual climatic events and to allow comparison of fluctuations between coasts.

This report is a refinement for 1976 of a similar report by Goulet (1978). His plots were for 1974 and 1975 only, as earlier data were not available in a computer compatible format. Subsequently, a computer tape of all available historical monthly mean temperature, density, and sea level data taken at NOS tide gage control stations was developed.² The Tides Branch of NOS provided update punch cards of monthly mean data. These data and certain Canadian data³ were merged with the historical tape for preparation of this report. The data are now archived by the National Oceanographic Data Center and are available through their Data Services Division.

McLain (1978) presented time series of monthly mean anomalies of SST's at coastal stations along the west coast of North America. Presented here are distance vs. time contours of long-term means and anomalies from the means for 1976 SST and density at selected

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² J. R. Goulet, Jr. and E. D. Haynes of the Resource Assessment Division, NMFS, NOAA, provided for the editing, keypunching, and quality control of these data.

³ L. F. Giovando, Environment Canada, Vancouver, B.C. V7V 1N6. Pers. commun.

stations along the coasts of North America (Appendix 10.1).

The 1976 data are presented as anomalies from a long-term mean for the period 1948-75. This reference period differs from the 1948-67 period used for other data sets such as maps of SST anomaly (McLain, Paper 9). The change was necessary to develop means for certain stations which were established in the last decade.

The stations used in this report are shown in Figure 10.1. The stations chosen were those which had the best combination of desirable characteristics: exposure to open ocean conditions, long data records, minimum gaps in data records, and equidistance between stations. The ideal combination seldom existed and consequently many of the stations used were in estuaries, had gaps in coverage, or were at varying intervals along the coast. For example, data coverage is poor in Oregon and Washington as all stations are in estuaries or are subject to river runoff (as at Neah Bay near the mouth of the Strait of Juan de Fuca). Good coverage was available from British Columbia lighthouses which have long complete data records from open, exposed locations.

The data are plotted as contoured isopleths of the long-term mean and anomaly by month and station position along the coast. Temperature data are in degrees Celsius while density data are in sigma-t units $[(\text{density}-1) \times 1000]$. Density values are computed for a standard water temperature of 15.0C. All monthly means represent at least 12 daily observations.

WEST COAST SEA SURFACE TEMPERATURES

The long-term monthly mean (1948-75) SST's at stations along the west coast of North America (Fig. 10.2) had minimum values in January and February and maximum values in July or August. Minimum winter temperature occurred at Kodiak, AK, while maximum summer temperature occurred at Los Angeles, CA. The winter minima occurred earlier (in January) at the southern stations (California to southern British Columbia) than at the northern stations, where minimum values occurred in February. Summer maxima occurred in August at all stations along the coast except at Neah Bay, WA, where the maximum occurred in July.

Bakun et al. (1974) described the long-term mean distribution of SST from ships in 1-deg squares of longitude and latitude adjacent to the west coast of the United States. Their data show that offshore SST minima and maxima occur about one month later than at the shore stations. This may result from more rapid warming in spring and cooling in fall in shallower coastal waters. The summer maximum temperatures reported by Bakun

et al. (1974) are similar to those at the coastal stations but winter minimum temperatures are about 1C lower at the coastal stations. This depression of coastal coastal temperatures may result from the lower heat capacity of the shallower water column at the coastal stations as compared to the offshore areas.

Both Figure 10.2 and the figure of Bakun et al. (1974) show a horizontal trend to the isotherms near Point Conception, CA, between Port San Luis and Los Angeles. This "flattening" of the isotherms is an indication of change of ocean water masses at Point Conception between the cold California Current water to the north and the warmer water of the Los Angeles Bight to the south.

During 1976 the anomalies of SST's at coastal stations were rather noisy and the only major trend was the presence of cooler than normal water along the coast during spring and summer from Sitka, AK, south to California. During summer, first in southeastern Alaska and later farther south, the anomalously cool water was replaced by warmer than normal water which reached maximum anomalies of +2.5C at Yakutat, AK, and off southern California in November and December.

The SST charts presented monthly in Fishing Information showed general negative anomalies of SST along the coast during 1976 until July when positive anomalies first impinged against the Oregon and southern California coasts. Positive anomalies spread during summer and fall and occurred along the entire coast in November and December, in agreement with the coastal station data.

WEST COAST DENSITIES

The long-term mean distribution of density along the west coast of North America (Fig. 10.3) showed that minimum densities occurred off California in February, probably in response to winter rains. In Alaska, however, minimum densities occurred in June or July due to snow and glacial melt.

During 1976, observations of density were spotty but showed positive anomalies off most of the coast most of the year. Large positive anomalies of density off San Francisco and Crescent City were associated with drought conditions existing over California most of the year. The low densities at Kodiak, AK, in August and September were apparently in response to local precipitation.

EAST COAST SEA SURFACE TEMPERATURES

The long-term mean SST's at stations along the east coast (Fig. 10.4) showed minimum temperatures at all stations January-March, and maximum temperatures July-September. As for the west coast, the peaks were earlier (January and July-August) at the southern stations and later (February-March and August-September) at the northern stations. Minimum winter temperatures of 0.6°C occurred in February at Portland, ME, and maximum summer temperatures of 30.7°C occurred in August at Key West, FL.

Two regions of rapid change of SST with distance can be seen (Fig. 10.4). These regions are between Kiptopeke Beach, VA, and Myrtle Beach, SC, and between Mayport and Miami Beach, FL. As at Point Conception on the west coast, these regions are associated with changes in ocean circulation and occur at Cape Hatteras and Cape Canaveral, respectively. Unlike Point Conception, however, where the greatest SST change between adjacent stations occurred in summer (4.0°C change in August), the greatest changes in SST between stations on the east coast occurred in winter or spring (8.2°C change in January at Cape Canaveral and 5.7°C in April at Cape Hatteras).

During 1976, sampling at the stations was incomplete and many values were missing. In January anomalies of SST were negative along the entire coast as were air temperatures over most of the eastern United States (Wagner 1976). Anomalous warming occurred in February, and by March SST's were above normal along the coast (up to 2.6°C above normal at Charleston, SC). This warming also was mentioned by Taubensee (1976a). During the summer months anomalies were positive at Montauk Point, NY, and to the north but were negative to the south. SST's were generally below normal during the fall, and became extremely cold in November as the unusually cold winter of 1976-77 began. An extreme negative anomaly of -5.5°C was observed at Sandy Hook, NJ, in November.

Chamberlin and Armstrong (Paper 5) summarized air temperature data along the east coast to show the development of the winter of 1976-77 when strong northerly winds occurred over much of the eastern United States. Their data, from National Weather Service weather stations for the period July 1976-January 1977, indicated that anomalies of air temperatures in fall 1976 were most negative during November over most of the coast. This is in agreement with the SST data. In neither the air temperature nor the SST data did large negative anomalies occur as far south as Miami or Key West, FL. Dickson (1977) also showed that southern Florida air temperatures were not unusually cold in November. The strong negative anomalies of SST in November were a response to the extremely southern location of the jet stream and the consequent cold, dry winds from the north and northwest. These

atmospheric conditions enhanced heat loss from the water, strengthened southward-flowing coastal currents, and increased vertical mixing. Evidently these processes were not fully effective at Miami and Key West where SST's are more closely associated with Gulf Stream advective processes.

EAST COAST DENSITIES

The long-term mean density data on the east coast (Fig. 10.5) show that many of the stations are affected by land runoff. Such runoff is particularly evident in the figure at Boston, MA, Sandy Hook, NJ, Kiptopeake Beach, VA, and Charleston, SC, where closed contours enclose regions of minimum water density. Minimum density water occurred at the northern stations March-May, while at the southern stations it occurred January-April. This delay in the time of minimum density at the northern stations resulted from retarded snowmelt and river discharge in spring in the north relative to winter precipitation in the south. The timing of maximum water density similarly is delayed to the north as maximum density generally occurred May-September at the southern stations and during September or October at the northern stations.

During 1976 density observations were frequently missing, and the available observations did not have much coherence from station to station or month to month. A region of coherent positive anomalies occurred from Montauk Point, NY, and north over most of the year, with the obvious exception of Boston, MA, and Portland, ME, during January-March. Positive density anomalies at Woods Hole, MA, and Montauk Point increased rather steadily during the year.

Large and variable anomalies occurred at Charleston, SC, and Mayport, FL, and resulted from fluctuations of river discharge near these stations. For example, the positive anomalies of density at these stations February-May were associated with drought during February and March (Dickson 1976a; Taubensee 1976a). Similarly the negative density anomalies at these stations in June were associated with higher than normal precipitation in the area (Dickson 1976b; Taubensee 1976b).

GULF OF MEXICO COAST SEA SURFACE TEMPERATURES

The long-term means of SST's at all stations along the U.S. coast of the Gulf of Mexico (Fig. 10.6) showed minimum values in January and maximum values in July or August. Minimum winter temperatures occurred at the most northern, estuarine station,

Dauphin Island, AL, and maximum summer temperatures occurred at the most southern, open ocean station, Key West, FL.

During 1976, observations of SST's at Gulf coast stations were fairly complete and showed good coherence in space and time. A pattern of SST anomalies similar to that observed at east coast stations from New Jersey to Florida occurred. SST's were anomalously cold at all Gulf coast stations during December 1975 and January 1976 with the greatest anomalies in Florida. Anomalous warming began in February in Texas, and SST anomalies peaked in March at Cedar Key, FL. Anomalous cooling then occurred over most of the area for the remainder of the year, peaking in the large negative anomalies of November over most of the coast. The negative anomalies in November were $<1^{\circ}\text{C}$ in magnitude only at Key West, FL. The greatest negative anomaly (-5.1°C) was at Galveston, TX, in November. Chamberlin and Armstrong (Paper 11) in their summary of Gulf coast air temperatures during late 1976 also found greatest negative anomalies at Galveston during November. The anomalies of air temperature were caused by strong northerly winds, whereas the SST anomalies were caused by heat losses to the cold, dry air.

GULF OF MEXICO COAST DENSITIES

Long-term mean water density (Fig. 10.7) ranged from almost fresh in January at Dauphin Island, AL (in Mobile Bay), to open ocean conditions at Key West, FL. The months of minimum and maximum densities varied and reflected variations in timing of local river discharge. Minimum densities occurred January-June and maximum densities occurred June-November.

Anomalies of density in 1976 were variable, and apparently were related to local fluctuations of precipitation and runoff. Negative anomalies of density were observed almost all year at south Texas stations. Positive anomalies occurred during August-October from Dauphin Island to Key West, and into December at stations in southern Florida.

SUMMARY

Although coastal station data are noisy and have frequent gaps in coverage, they do show large-scale coherences among stations. These coherences are in general caused by climatic fluctuations that affect long stretches of coastline. An extreme example of such a climatic change is the strong northerly winds over much of the eastern United States during November 1976. These winds created negative anomalies of SST at coastal stations of at least

-1C in magnitude from Portland ME, to Mayport, FL, and from St. Petersburg, FL, to Padre Island, TX. Extreme anomalies of -5.5C were observed at Sandy Hook, NJ, and -5.1C at Galveston, TX, in November.

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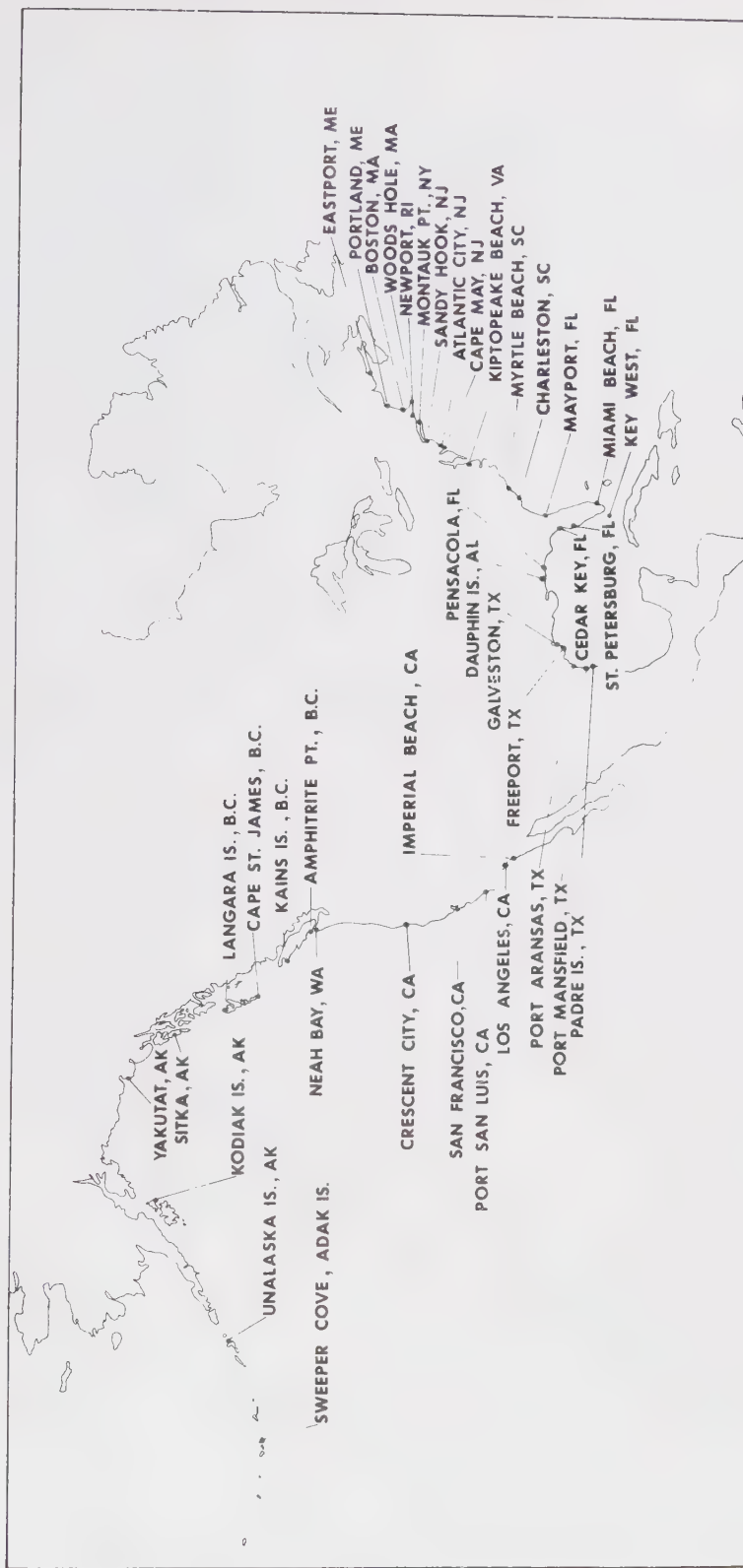
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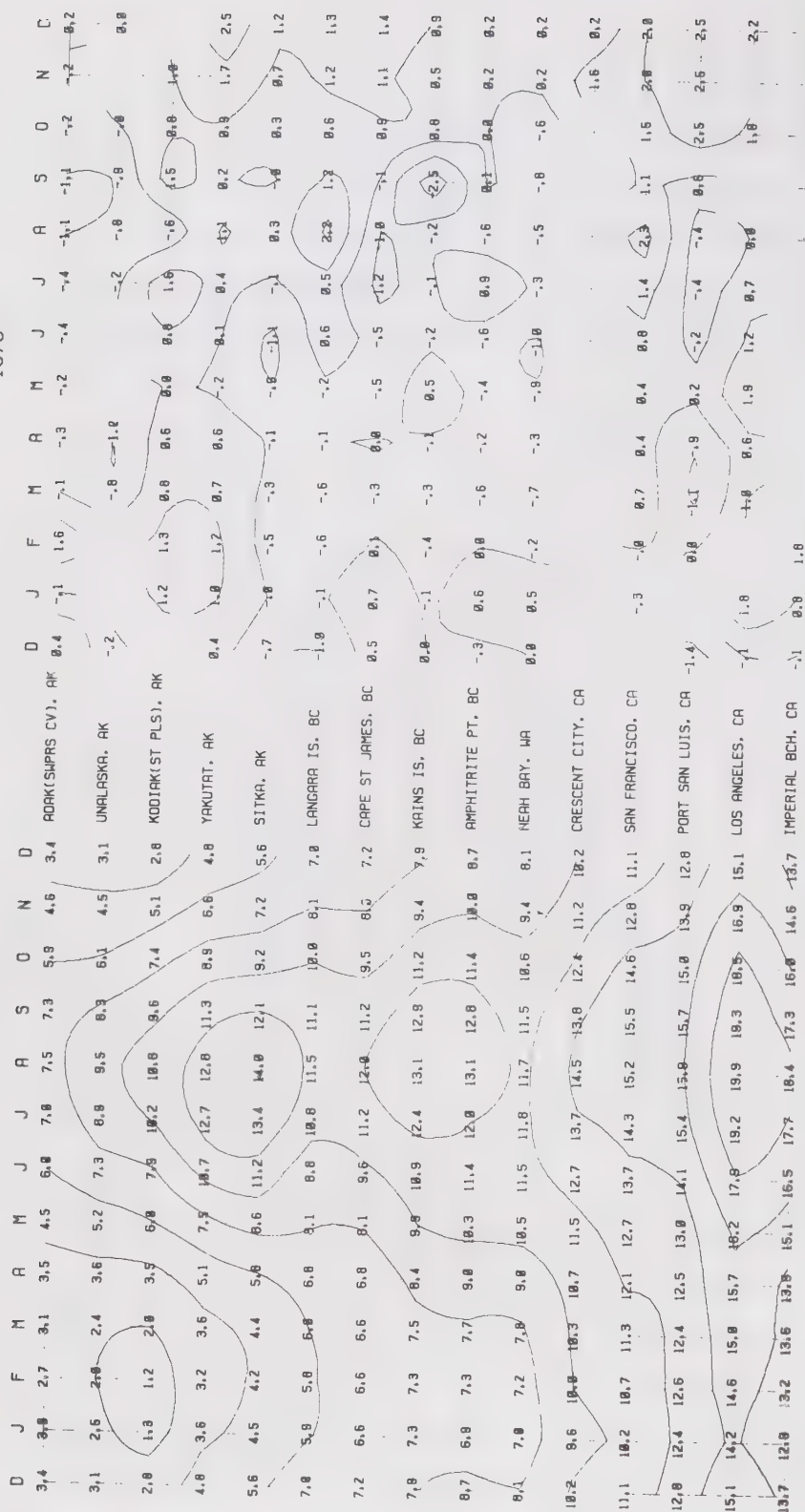


Figure 10.2.—Long-term mean for 1948-75 (left) and anomalies for 1976 (right) of sea surface temperature (degrees C) along the U.S. west coast. Contour intervals are 2.0C for mean and 1.0C for anomalies.

1976

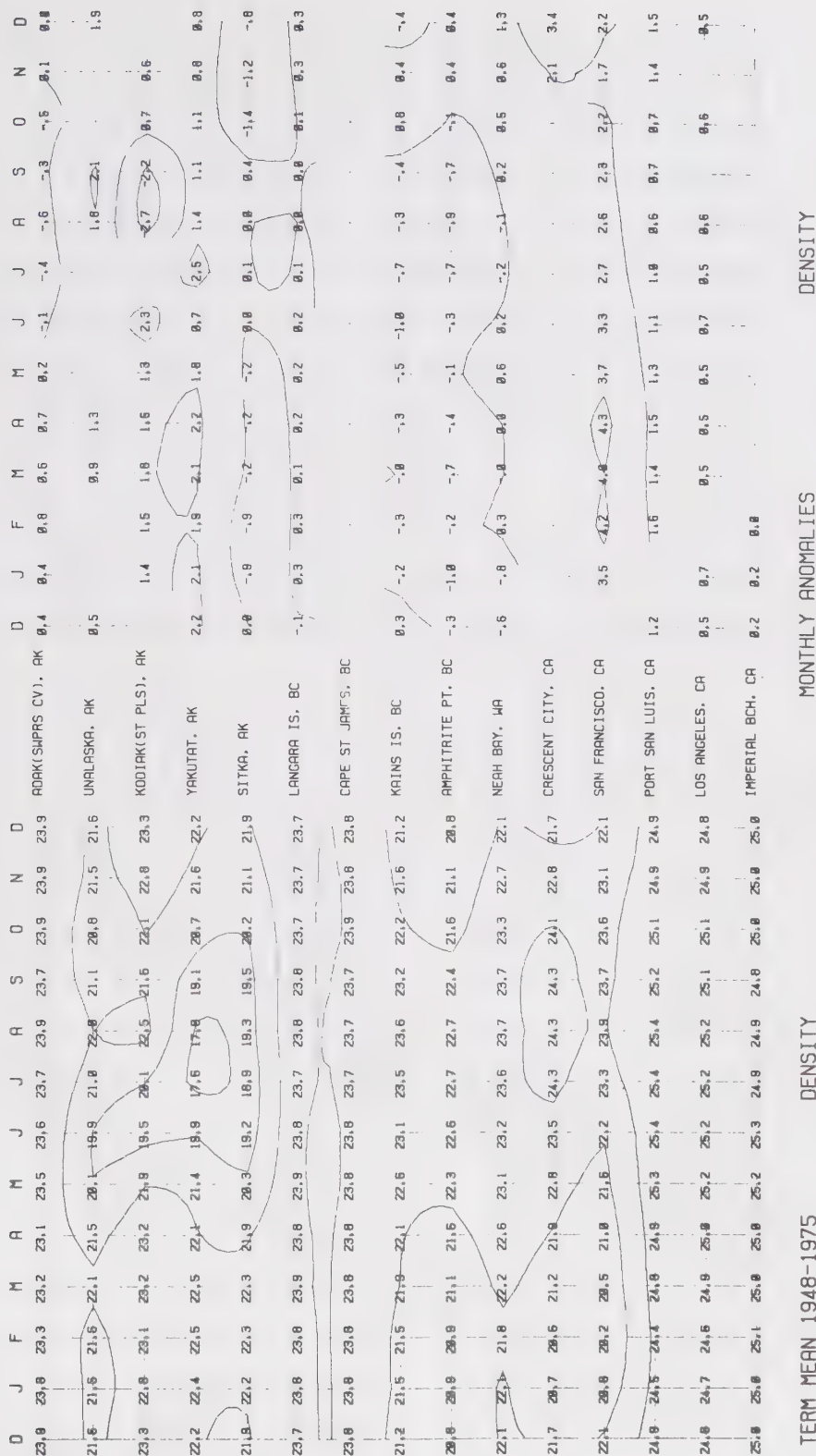
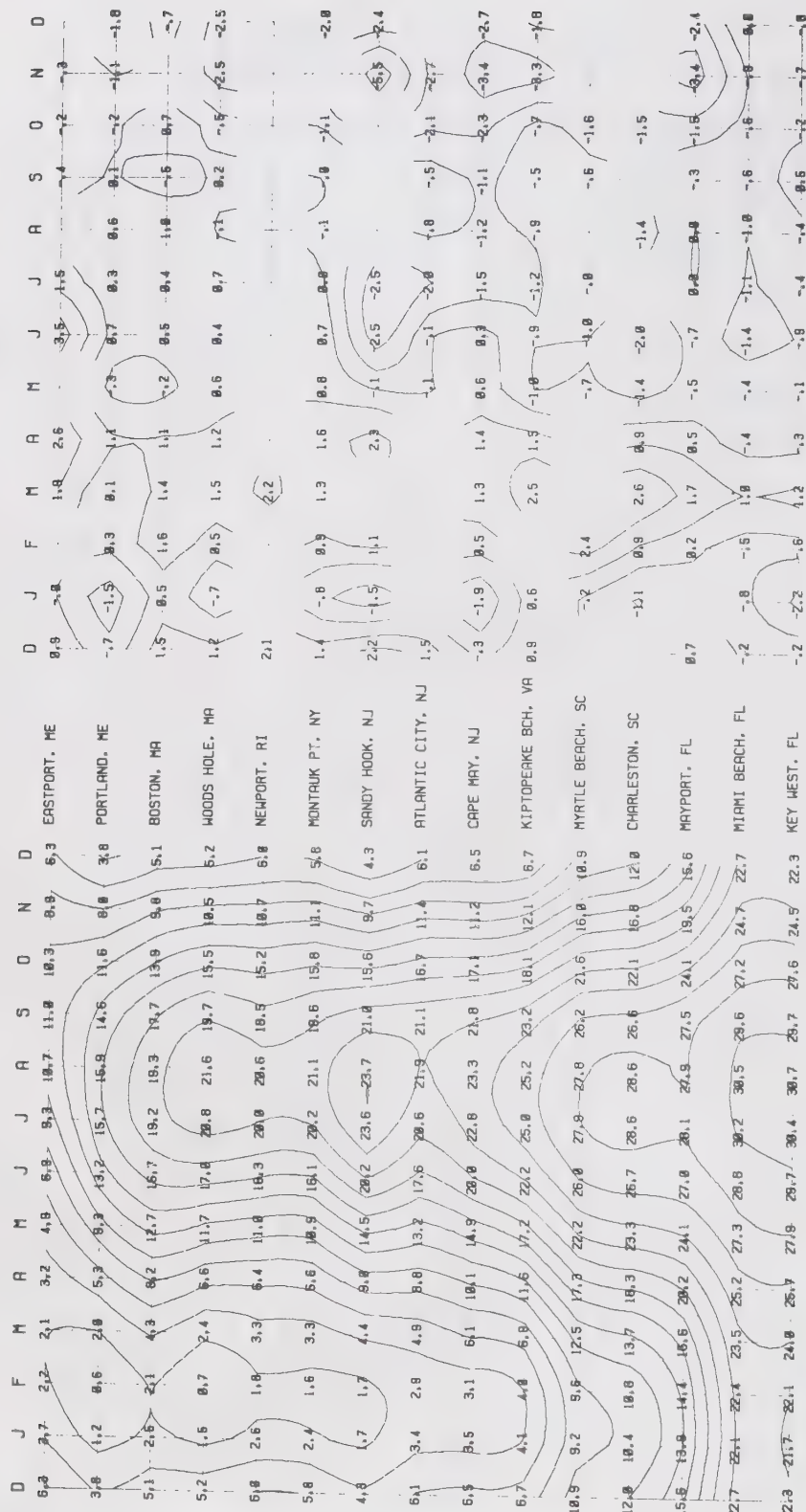


Figure 10.3.—Long-term mean for 1948-75 (left) and anomalies for 1976 (right) of density (sigma-t) along the U.S. west coast. Contour interval is 2 units.

1976



TERM MEAN 1948-1975

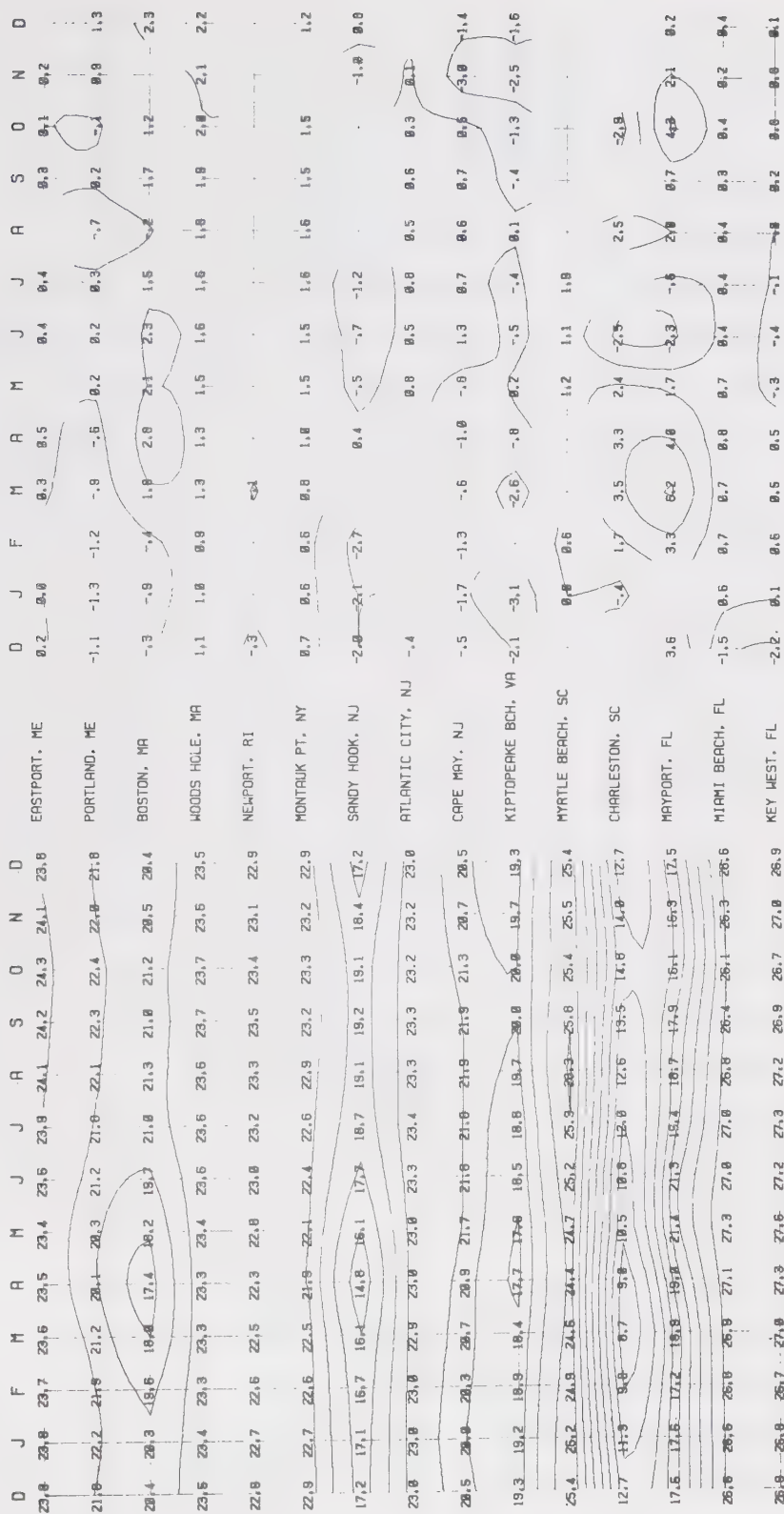
SEA TEMP

MONTHLY ANOMALIES

SEA TEMP

Figure 10.4—Long-term mean for 1948-75 (left) and anomalies for 1976 (right) of sea surface temperature (degrees C) along the U.S. east coast. Contour intervals are 2.0C for mean and 1.0C for anomalies.

1976



DENSITY

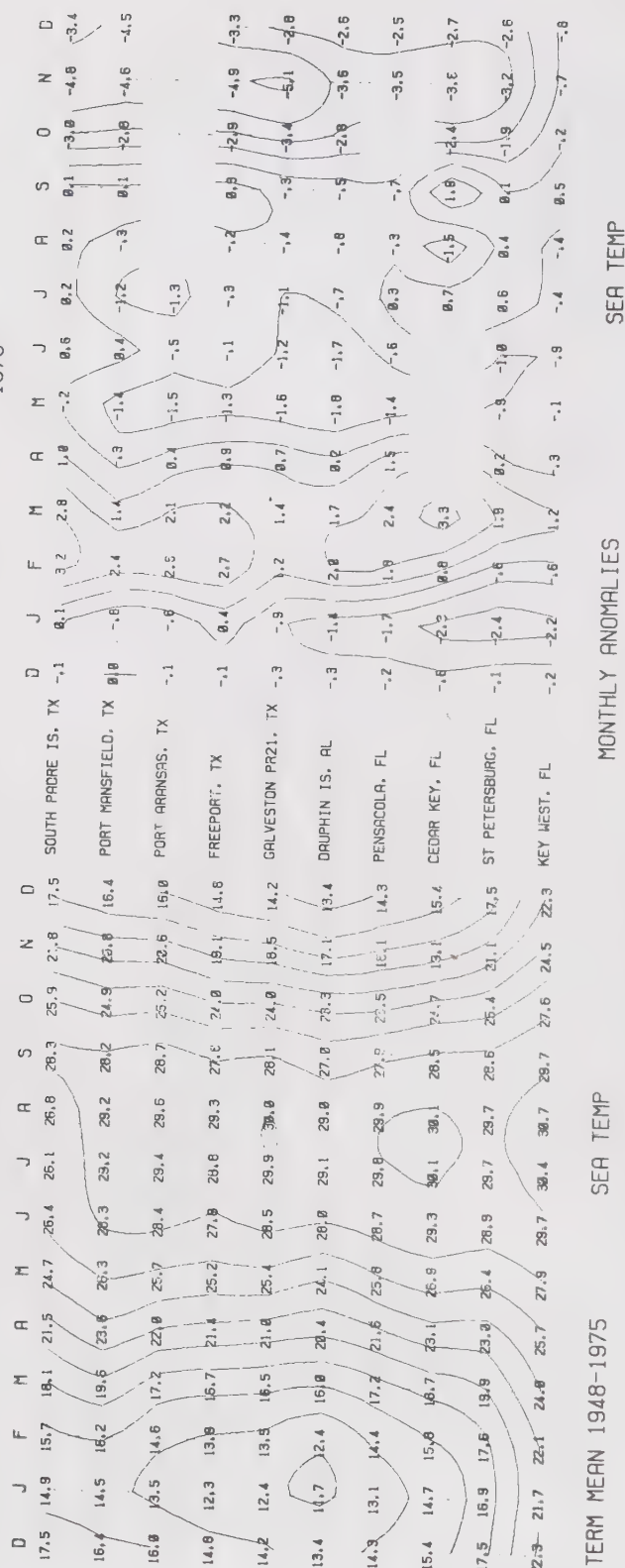
MONTHLY ANOMALIES

DENSITY

TERM MEAN 1948-1975

Figure 10.5.—Long-term mean for 1948-75 (left) and anomalies for 1976 (right) of density (sigma-t) along the U.S. east coast. Contour interval is 2 units.

1976



TERM MEAN 1948-1975

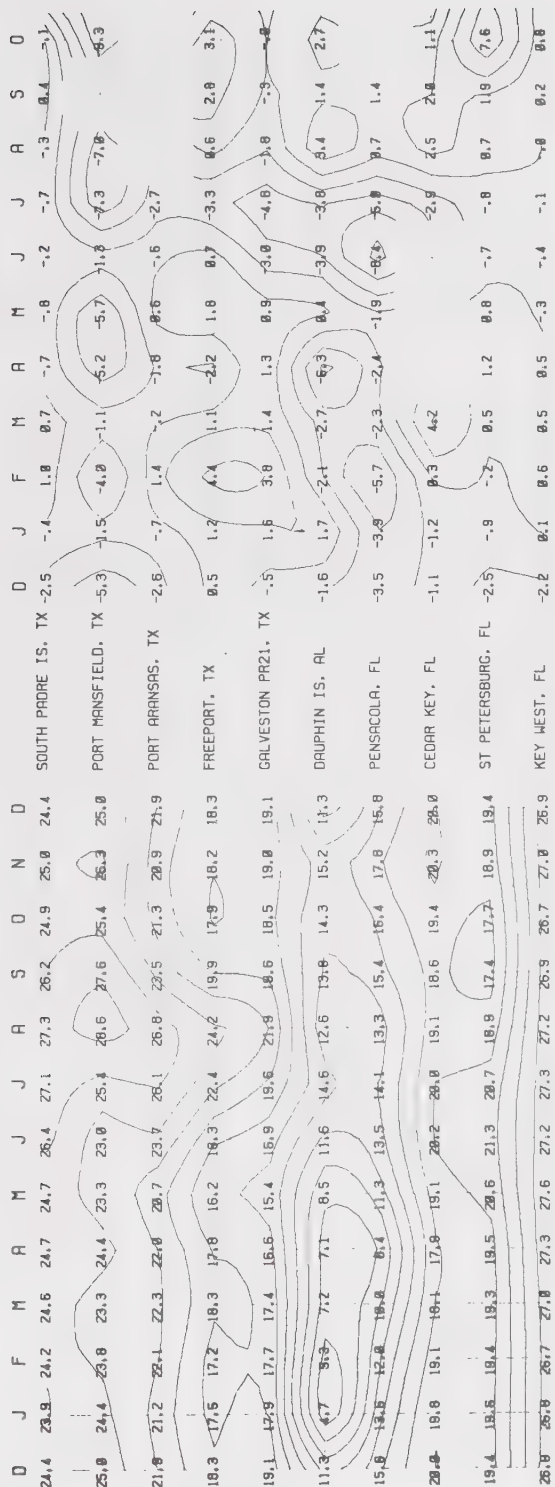
SEA TEMP

MONTHLY ANOMALIES

SEA TEMP

Figure 10.6.—Long-term mean for 1948-75 (left) and anomalies for 1976 (right) of sea surface temperature (degrees C) along the U.S. Gulf coast. Contour intervals are 2.0C for mean and 1.0C for anomalies.

1976



DENSITY

MONTHLY ANOMALIES

DENSITY

TERM MEAN 1948-1975

Figure 10.7.—Long-term mean for 1948-75 (left) and anomalies for 1976 (right) of density (sigma-t) along the U.S. Gulf coast. Contour interval is 2 units.

Locations of stations shown in Figure 10.1.

West Coast

Adak, AK	51N52°	176W39°
Unalaska, AK	53N53°	166W33°
Kodiak, AK	57N45°	152W29°
Yakutat, AK	59N33°	139W44°
Sitka, AK	57N03°	135W21°
Langara Island, B.C.	54N15°	133W04°
Cape St. James, B.C.	51N56°	131W01°
Kains Island, B.C.	50N27°	128W02°
Amphitrite Point, B.C.	48N55°	125W32°
Neah Bay, WA	48N22°	124W37°
Crescent City, CA	41N45°	124W12°
San Francisco, CA	37N48°	122W28°
Port San Luis, CA	35N10°	120W45°
Los Angeles, CA	33N43°	118W16°
Imperial Beach, CA	32N35°	117W08°

East Coast

Eastport, ME	44N54°	66W59°
Portland, ME	43N40°	70W15°
Boston, MA	42N21°	71W03°
Woods Hole, MA	41N32°	70N40°
Newport, RI	41N30°	71W20°
Montauk, NY	41N03°	71W58°
Sandy Hook, NJ	40N28°	74W01°
Atlantic City, NJ	39N21°	74W25°
Cape May, NJ	38N58°	74W58°
Kiptopeke Beach, VA	37N10°	75W59°
Myrtle Beach, SC	33N41°	78W53°
Charleston, SC	32N47°	79W56°
Mayport, FL	30N24°	81W26°
Miami Beach, FL	25N46°	80W08°
Key West, FL	34N33°	81W49°

Gulf of Mexico Coast

Padre Island, TX	26N04°	97W09°
Port Mansfield, TX	26N33°	97W26°
Port Aransas, TX	27N49°	97W04°
Freeport, TX	28N57°	95W19°
Galveston, TX	29N18°	94W47°
Dauphin Island, AL	30N15°	88W05°
Pensacola, FL	30N24°	87W13°
Cedar Key, FL	29N08°	83W02°
St. Petersburg, FL	27N46°	82W37°
Key West, FL	24N33°	81W49°

Marine Environmental Conditions off the Pacific Coast of the United States, January 1977-March 1978

D. R. McLAIN, F. FAVORITE, and R. J. LYNN

Introduction

During 1977 and early 1978 unusual atmospheric circulation occurred over the northeast Pacific. In both winters (1976-77 and 1977-78) strong and persistent high pressure ridges in the atmospheric circulation formed over the west coast of North America. The atmospheric circulation had a variety of effects on local oceanographic conditions and fishery resources in the region.

As a result of the ridge circulation during both winters, southerly winds of moist, warm air blew over Alaska and the eastern Bering Sea. This caused the coastal waters of the southeastern Bering Sea and the western Gulf of Alaska to be much warmer than normal. The warm weather broke a 6-year cold spell (1971-76) which had had serious effects on fisheries in the Kodiak Island region and the southeastern Bering Sea. The warm waters of 1977-78 should allow rapid growth of juvenile salmon, halibut, and other species. Herring spawning may be advanced by 1-2 weeks. Abundant precipitation fell over Alaska. Wind

driven surface transport caused surface waters to be held near the coast of the Gulf of Alaska. This convergence combined with the dilution from precipitation and runoff to increase coastal longshore circulation in the Gulf. Increased advection of waters from the south transported salpae into waters off southeastern Alaska in May and June 1978.

Off the west coast of the contiguous United States, the circulation associated with the atmospheric pressure ridges was dissimilar in the two winters. During the winter of 1976-77, a high pressure system persisted off the California coast which diverted storms to the north. Calm, clear weather under this high pressure system produced record drought over California and warmed coastal waters. Upwelling off the California coast was moderate.

In contrast, during the winter of 1977-78 the ridge over Alaska moved northwestward, the high pressure system off California was absent, and a weak trough occurred off the west coast. The trough allowed storms to come into the coastal zone and bring abundant precipitation to California, breaking the drought. Airflow was more southerly than normal causing coastal convergence and possibly increased flow of the Davidson Current. Occasional strong downwelling pulses occurred. The coastal convergence broke a 5-year run of strong upwelling. Due to the convergence and to possibly increased Davidson Current, coastal waters were again warmer than normal. Also due to the

coastal convergence, eggs of winter spawners such as anchovy would have been held nearer the coast than normal and may result in better than normal survival.

Cooler than normal water occurred throughout the period in an extensive area of the central North Pacific near lat. 40°N and long. 150°W. Strong winds over this region during the winter of 1976-77 appear to have strengthened the transport of the West Wind Drift Current. Low salinity water occurred in the California Current during 1977 and especially so in 1978, suggesting anomalously great advection of low salinity, subarctic water from the north and increased local precipitation. Associated with this change was a weakening of salinity fronts of the Transition Zone in 1977. Fronts in the Transition Zone in early 1978 were near normal.

Sea surface temperatures in the eastern tropical Pacific decreased during early 1977 from the anomalously high temperatures that resulted from a moderate El Niño in 1976. Sea surface temperatures were lower than normal off Peru and along the Equator from April to September 1977 and during early 1978, possibly due to increased upwelling. Temperatures off Baja California were above normal in early 1977 due to excess solar insolation and were again above normal in early 1978 due to weak upwelling. Wind mixing and tropical storms reduced surface water temperatures along the coast of Central America during 1977 and early 1978. Strong winds and the response of tuna fishermen to porpoise regulations contributed to below normal tuna catches during 1977.

Atmospheric Variations

The dominant feature of the atmospheric circulation over the northeast Pacific Ocean during January 1977 to March 1978 was the presence during the winters of 1976-77 and 1977-78 of persistent and intense ridges of high atmospheric pressure over the west coast of North America. The January circulation, as depicted by the heights of the 500-mb pressure surface, is

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Fishery technicians (left and right above) launch instruments to measure oceanographic conditions. Temperature and salinity variations reveal such important ocean processes as upwelling, ocean front formation, and current changes. Yellowfin tuna (bottom right), ranging across broad reaches of the eastern tropical Pacific Ocean, are sensitive to specific ranges of temperature and oxygen. Fishermen monitor the vertical ocean temperature structure as an important tactic in fishing for them.

representative of each winter (Fig. 1). The upper air ridges resulted in the advection of warm, maritime air northward over the northeast Pacific and brought southerly winds and mild conditions to the south coast of Alaska. A persistent blocking high pressure cell was present off California during much of 1977 and diverted storms to the north. During the winter of 1977-78 the ridge structure was expanded and shifted to the northwest over Siberia and Alaska and a weak low pressure trough was present off the west coast. Southwesterly winds associated with this trough then brought storms onto the west coast of the United States. Downstream from the persistent ridges along the west coast northerly winds blew over the eastern United States, producing record cold and snowy winters. The ridges in both winters were somewhat similar to the ridge that occurred during the winter of 1957-58 which brought warm coastal waters to much of the west coast of North America and cold weather to the eastern United States (Johnson and McLain, 1975). Namias (1978) described the unusual atmospheric circulation of the winter of 1976-77, its relations to ocean conditions, and multiple causes for its formation.

At the ocean surface, beneath the ridges of upper air circulation, the distribution of surface barometric pressure indicates the surface winds which drive the ocean currents. Figures 2, 3 show the surface pressure patterns and winds over the Northeast Pacific during the winters of 1976-77 and 1977-78 (January data are again taken as representative). The Aleutian low pressure system is the dominant winter feature of the surface circulation over the North Pacific and in both winters the Aleutian low was deeper than normal (Fig. 2, 3, lower). This anomaly of low pressure had been characteristic of the last quarter of 1976 and lasted through February 1977. The anomaly pattern became reestablished in January 1978 and lasted through April.

During the 1976-77 winter the normally weak high pressure cell of California was elongated and extended northward over Oregon, Washington,

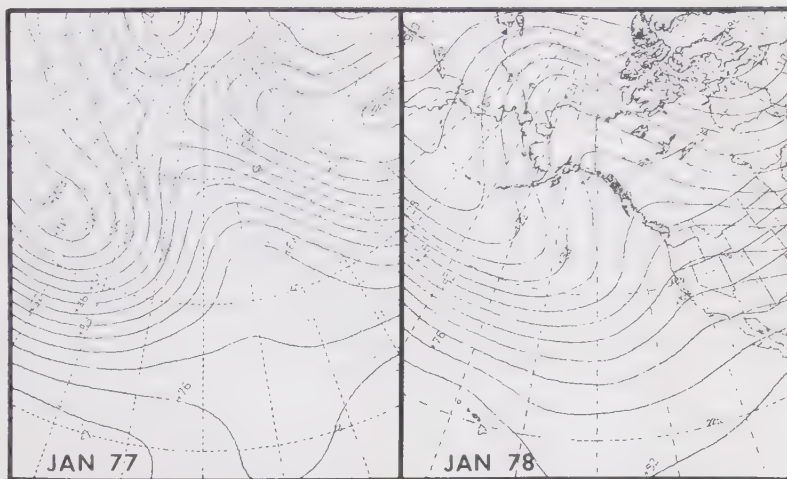


Figure 1.—Heights of 500-mb pressure surface (in tens of meters, +5,000 m) in January 1977 and January 1978. Contour lines are at 60-m intervals.

and British Columbia (Fig. 2, upper). The resulting intensified atmospheric circulation advected warm maritime air toward the southern Alaska coast where record mild temperatures and abundant rainfall occurred. Under the high pressure cell, winds were weak, clear weather prevailed, and record drought occurred in California.

In the winter of 1977-78, a deepened Aleutian low extended far to the east of its normal position and the high pressure cell off California was absent (Fig. 3, upper). This circulation directed storms over the west coast of the United States and resulted in record or near record rainfall, breaking the California drought. During the intervening seasons, barometric pressure patterns and associated winds were closer to normal than during the winters.

Gradient and Vector Winds

The relative intensity and direction of surface winds over the northeast Pacific during the winters of 1976-77 and 1977-78 is shown by isolines of surface barometric pressure and their gradients (Fig. 2, 3). Also shown in the figures are arrows, which in the upper half of the figures represent the direction of resultant average vector

winds and in the lower half of each figure represent the departure of each vector wind from its long-term average.

The westerly winds south of the deepened Aleutian low were stronger than normal west of long. 150°W in the last quarter of 1976 and first 2 months of 1977 (e.g., January 1977, Fig. 2). Between long. 130° and 150°W there was a strong southerly component to the winds and the general marine conditions were characterized by high winds, high seas, and storms. East of long. 130°W, conditions were relatively mild. By March the subtropical high pressure cell off California had intensified, producing strong northerly winds along the coastal region and causing a strong pulse of coastal upwelling from Baja California northward to Alaska. Winds were near normal over extensive areas of the eastern North Pacific Ocean through July. For 3 months beginning in August the Aleutian low alternated between a deepened and relaxed condition in the area west of long. 135°W. East of long. 135°W winds were near normal. In December, a southeastward shift of the Aleutian low and a weakening of the high pressure cell brought southerly moist winds to the California coastal regions.

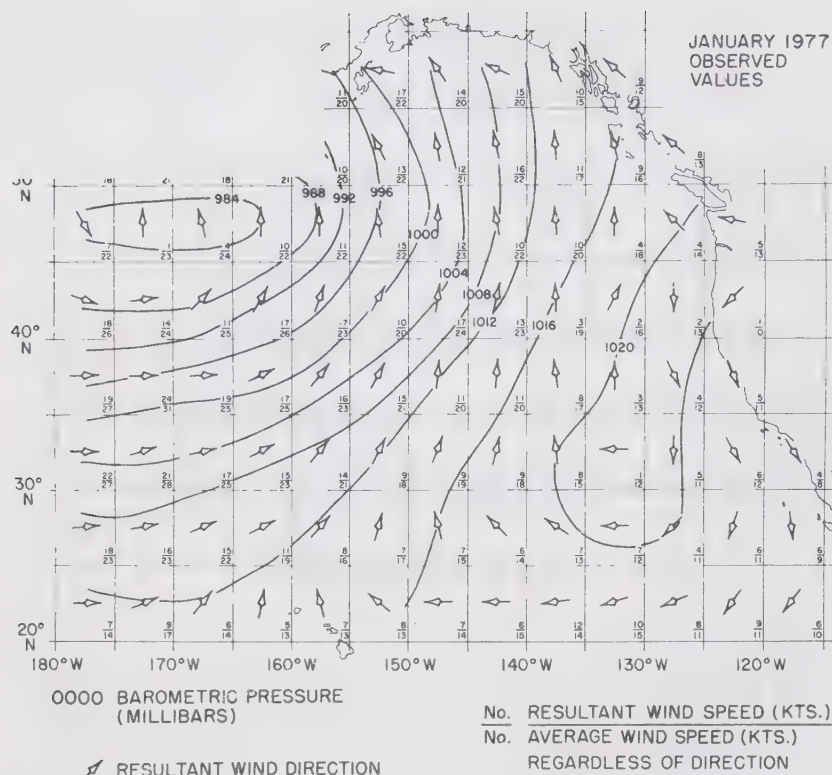
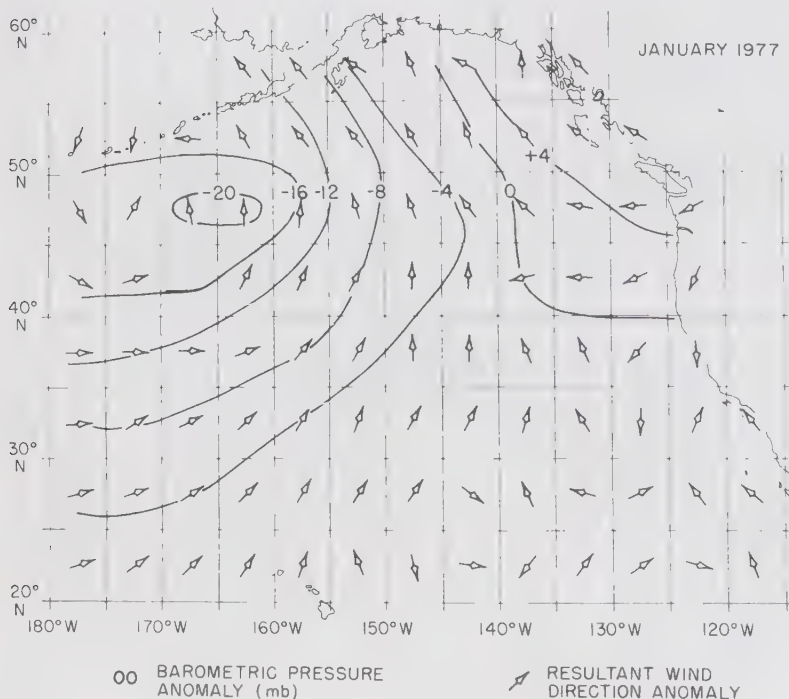


Figure 2.—Upper—Sea level barometric pressure (millibars), resultant wind direction (degrees true), resultant wind speed (knots), and average wind speed (knots) regardless of direction for January 1977 (from *Fishing Information*). Lower—Departure of sea level pressure (millibars) from the long-term mean (calculated from 1961 through present year) and departure of resultant wind direction from long-term mean for January 1977 (courtesy of J. Renner).

Ocean Surface Transport and Upwelling

The polar easterlies, mid-latitude westerlies, and subtropic easterlies (trades) are terms describing long-term averages of prevailing winds over the oceans. Beneath these zonal regions of winds lie the major ocean currents that flow over great distances in much the same direction as the winds. In the northeast Pacific the major wind driven currents are the West Wind Drift Current, the Alaskan Stream, the California Current, and the North Equatorial Current. The surface layer transports associated with these currents has been computed from classical Ekman theory based upon monthly average wind data.¹ Although Ekman transport estimates form only a portion of the total ocean circulation, they suggest the monthly and seasonal influence of the winds. The 20-year averages of monthly transports at each of four selected locations in the northeast Pacific during 1977 and early 1978 are shown in Figure 4.

In the offshore region (e.g., lat. 39°N, long. 149°W; Fig. 4, lower), strong westerlies in winter strengthen the West Wind Drift. At lat. 27°N, long. 140°W subtropic easterlies may strengthen the North Equatorial Current in summer. During January and February of both 1977 and 1978



¹Computations of surface layer transport prepared by Andrew Bakun, Pacific Environmental Group, NMFS, NOAA, Monterey, CA 93940. Values are computed on a grid of 3° latitude and longitude from data of Fleet Numerical Weather Central, Monterey, CA 93940.

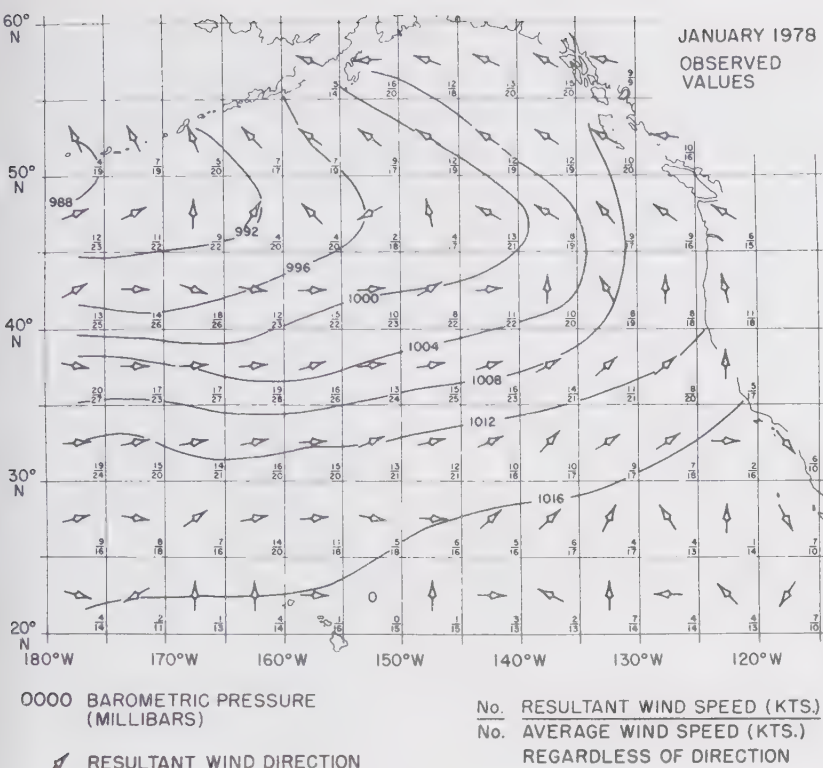
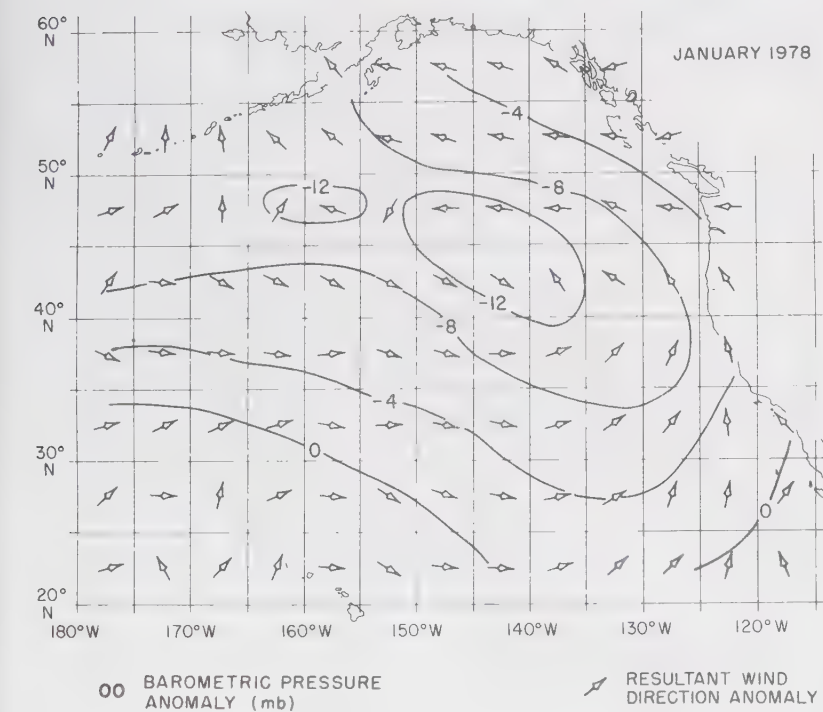


Figure 3.—Upper—Sea level barometric pressure (millibars), resultant wind direction (degrees true), resultant wind speed (knots), and average wind speed (knots) regardless of direction for January 1978 (from *Fishing Information*). Lower—Departure of sea level pressure (millibars) from the long-term mean (calculated from 1961 through present year) and departure of resultant wind direction from long-term mean for January 1978 (courtesy of J. Renner).



(Fig. 4, upper) transport at lat. 39°N, long. 149°W was very large and directed to the southeast. At lat. 27°N, long. 140°W where southeast winds normally drive the waters to the north, the transport for the same time periods was weak or southward. Thus in both winters and over a broad offshore region, the winds acted to intensify the West Wind Drift Current and the southeastward flow of the California Current. Low salinities in the California Current (discussed in a later section) may have, in part, been a result of greater than normal intrusion of subarctic waters, caused by strengthened advection. Transport during the intervening months was near normal with the exception of March 1977 at lat. 27°N, long. 140°W when the intensified subtropical high strengthened the southeast trades, producing large transport toward the northwest.

Along the coast, surface transport moves water onto or away from the coast and causes vertical movements of water known as upwelling (or downwelling)—a process of great biological significance. The northwest winds prevailing in summer along the coast from Oregon southward to Baja California (e.g., lat. 39°N, long. 127°W) cause surface transport offshore and replacement by cold, nutrient rich water upwelled from below. The nutrients in this water support the abundant biological productivity in the area. Along the Alaska coast (e.g., lat. 57°N, long. 140°W) transport is onshore during much of the year.

Onshore-offshore transports also affect the strength of coastal currents.

The effect of upwelling (and downwelling) forces a compensatory flow elsewhere in the water column which affects the density structure (baroclinicity) and, hence, geostrophic flow. In periods of increased coastal upwelling where there is anticyclonic flow (i.e., California Current) the flow is strengthened, and in periods of increased coastal downwelling where there is cyclonic flow (i.e., Alaskan Stream) the flow is similarly strengthened.

Transports computed for 1977 and early 1978 for the coast of northern California at lat. 39°N , long. 128°W show that there was anomalous offshore transport during March, June, and July 1977 and anomalous offshore transport during December 1977 through February 1978. Thus during March, June, and July there was increased upwelling and, possibly, a strengthened California Current near the coast. During the subsequent winter there was downwelling and possibly a stronger nearshore countercurrent. During a typical winter, the current seasonally weakens and shifts away from the coast while the poleward flowing California Undercurrent surfaces as a countercurrent (Davidson Current) in the near-coastal regions. In the subject winters each of these events may have been enhanced. One consequence of the onshore transport during early 1978 would have been to hold eggs and larvae of winter spawning fish such as anchovy closer to the coast than normal. This may be desirable for good survival.²

In the Gulf of Alaska at lat. 57°N , long. 140°W , winds during both winters acted to strengthen the normal seasonal onshore transport, strengthen coastal downwelling, and probably also enhance westward geostrophic flow in the Gulf of Alaska. The abundant precipitation of both winters caused dilution of coastal surface waters in the area and probably acted to further strengthen the enhanced

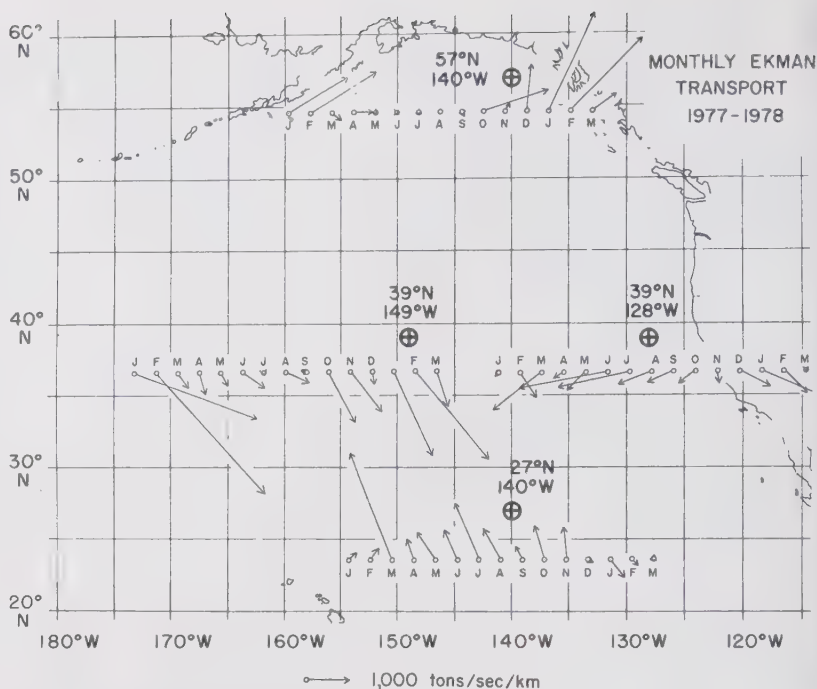
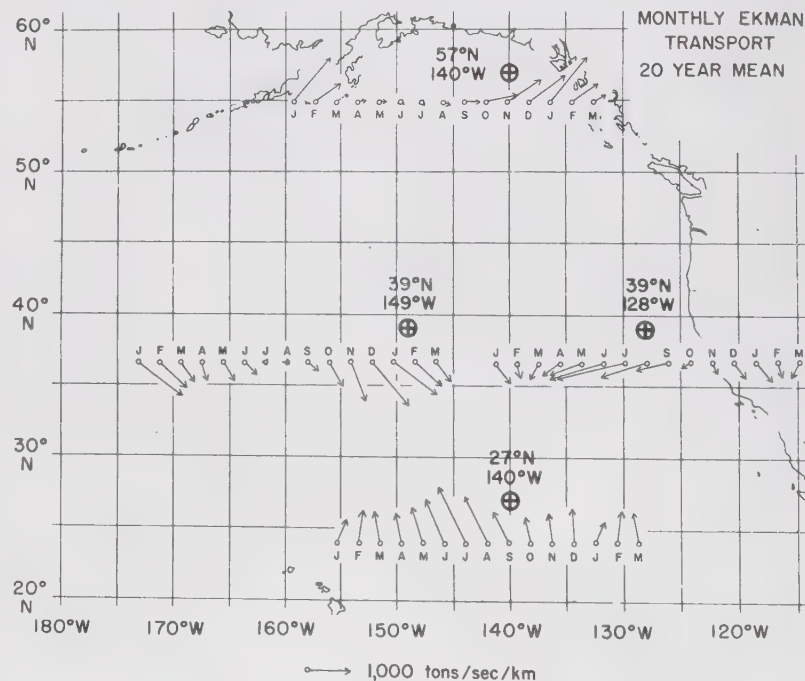


Figure 4.—Vectors of monthly Ekman transport for four areas of the eastern North Pacific, computed over a 3° square of latitude and longitude for January 1977 through March 1978 (upper) and for monthly means over a 20-year period (lower).



²Parrish, R. H., and C. S. Nelson. 1976. Larval transport mechanisms in the California Current. Presented at California Cooperative Oceanic Fisheries Investigations Conference, Indian Wells, Calif., November 16-18, 1976.

flow. Observations of clear, warm oceanic waters with abundant salpae off southeastern Alaska during May and June 1978³ are explained by the increased flow.

The details of variations of upwelling with distance along the coast are of particular interest. Bakun (1973) has computed the component of Ekman transport normal to the coastline as an index of the intensity of upwelling. This computation is made at 15 points along the coast from lat. 21°N off Mexico to lat. 60°N on the south coast of Alaska. Time-space variations of the upwelling as indicated by the upwelling index are shown in Figure 5 as percentiles of historic normal values.

Very strong upwelling occurred off northern California during January to November 1977. Upwelling index values at lat. 39°N for March, June, and July of 1977 were the highest for those months in the 32-year (1946-77) period of record. Only in May and after November did the values at lat. 39°N fall below the median for the month. Thus 1977 continued an unprecedented series of 5 years of strong upwelling off northern California which had begun in 1973.

In contrast to the generally strong upwelling of 1977, during early 1978 downwelling occurred along the California coast as previously mentioned. This downwelling is indicated on Figure 5 as extremely weak upwelling. The downwelling period broke the run of 5 years of strong upwelling mentioned above. The downwelling or weak upwelling began in December 1977 off California and extended along the entire coast from lat. 24° to 60°N, except for a minor peak in March at lat. 45° to 48°N. Off central California (lat. 30° to 36°N) the upwelling index was the lowest that had occurred during the period of historical record at 6 month-locations.

The upwelling off southern Baja California (at lat. 21°N and to a lesser extent at lat. 24°N) was persistently

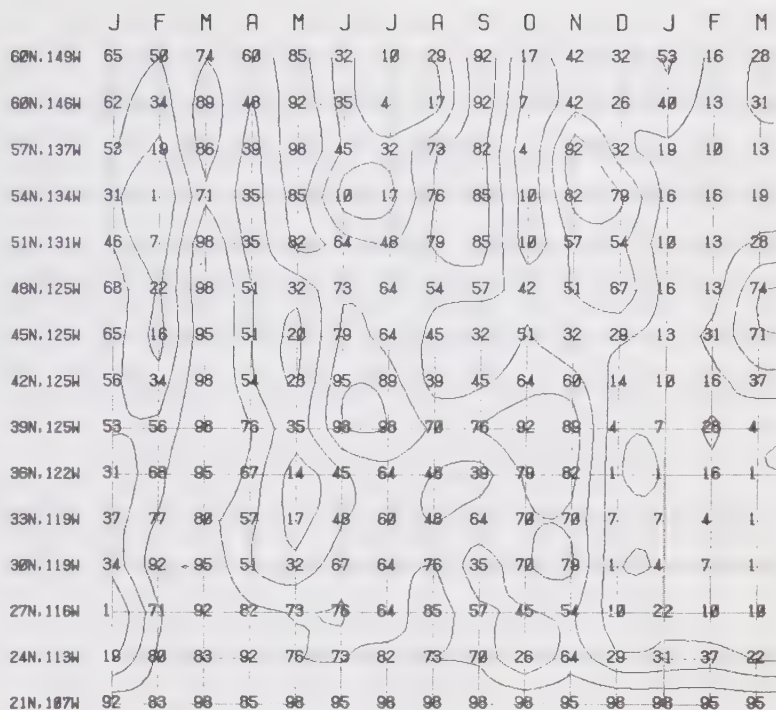


Figure 5.—Monthly upwelling index values for January 1977 to March 1978, in percentiles of the frequency distributions made up of the 32 values for each month and location in a 32-year (1946-77) time series. Locations in the Gulf of Alaska are toward the top of the figure; those off Baja California are toward the bottom. The contour interval is 25 percentiles. Values above the 50th percentile indicate stronger than normal upwelling while those below indicate weaker than normal upwelling.

strong throughout the period. During February to August, upwelling index values at lat. 27°N and southward have been in or near the upper quartile of the various month-location distributions. At the southermost point (lat. 21°N) the index was in the 95th or higher percentile throughout the period.

Widespread anomalies occurred in March and May 1977. Very high upwelling index values during March extended south of lat. 21°N off southern Baja California to lat. 60°N in the northern extremity of the Gulf of Alaska (where they indicate abrupt relaxation of the winter downwelling situation). During May, values were very low from off the Washington coast southward to northern Baja California but high in the Gulf of Alaska and off southern Baja California.

Sea Surface Temperature

Over the North Pacific, sea surface temperature (SST) increases predominately from north to south (Fig. 6). The nearly zonal pattern of isotherms of SST over the North Pacific mid-latitudes is deflected near the west coast by advection and upwelling. There is a northward bending of isotherms into the Gulf of Alaska and a southward bending from Oregon to Baja California. The deflection is greatest in summer months.

Over much of the open ocean in temperate latitudes the annual minimum in SST is reached during March (Fig. 6, upper) and the maximum is reached during September (Fig. 6, lower). The amplitude of the seasonal variation of sea surface temperature ranges from a high of about 10°C in

³Bruce L. Wing, Northwest and Alaska Fisheries Center, NMFS, NOAA, Auke Bay, AK 99821, pers. commun.

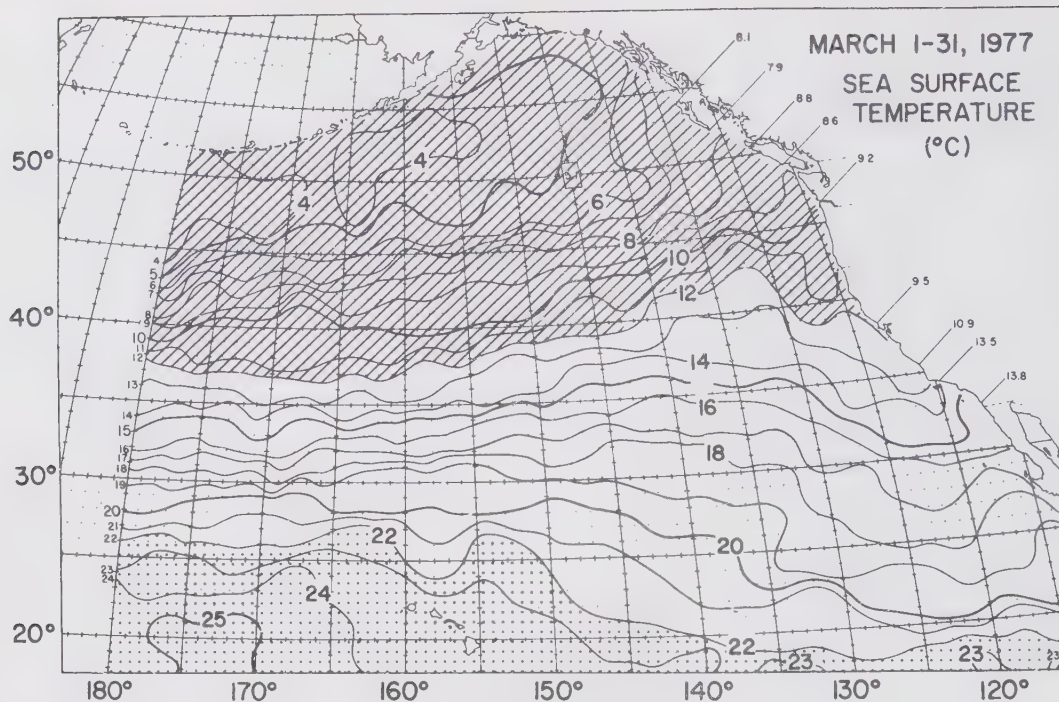
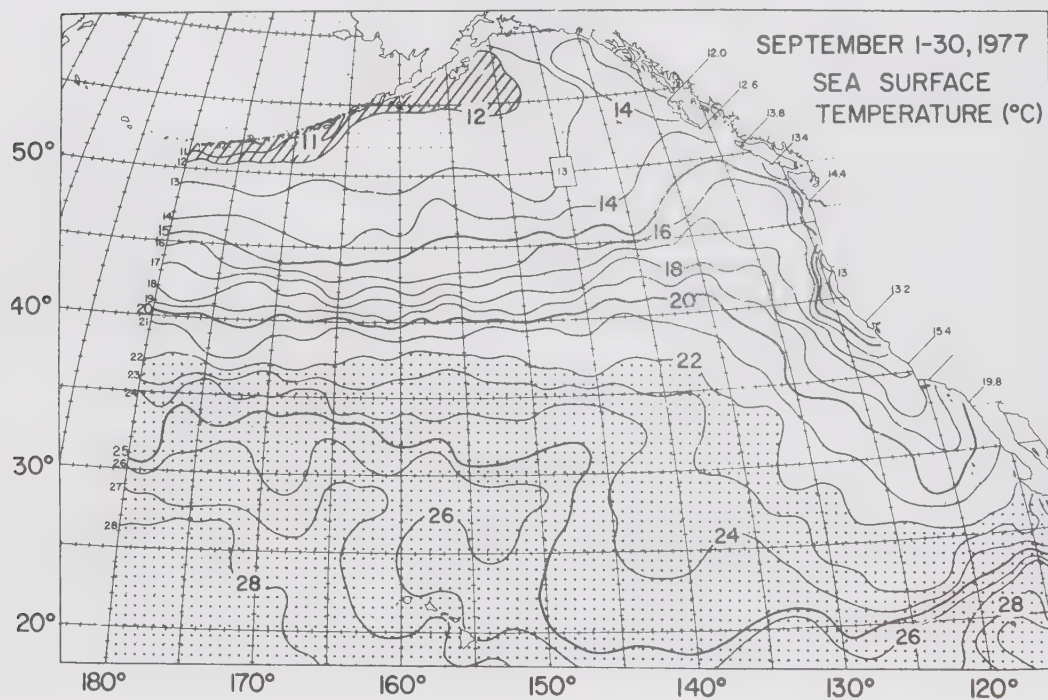


Figure 6.—Sea surface temperature for the eastern North Pacific during March 1977 (upper) and September 1977 (lower), adapted from *Fishing Information*.



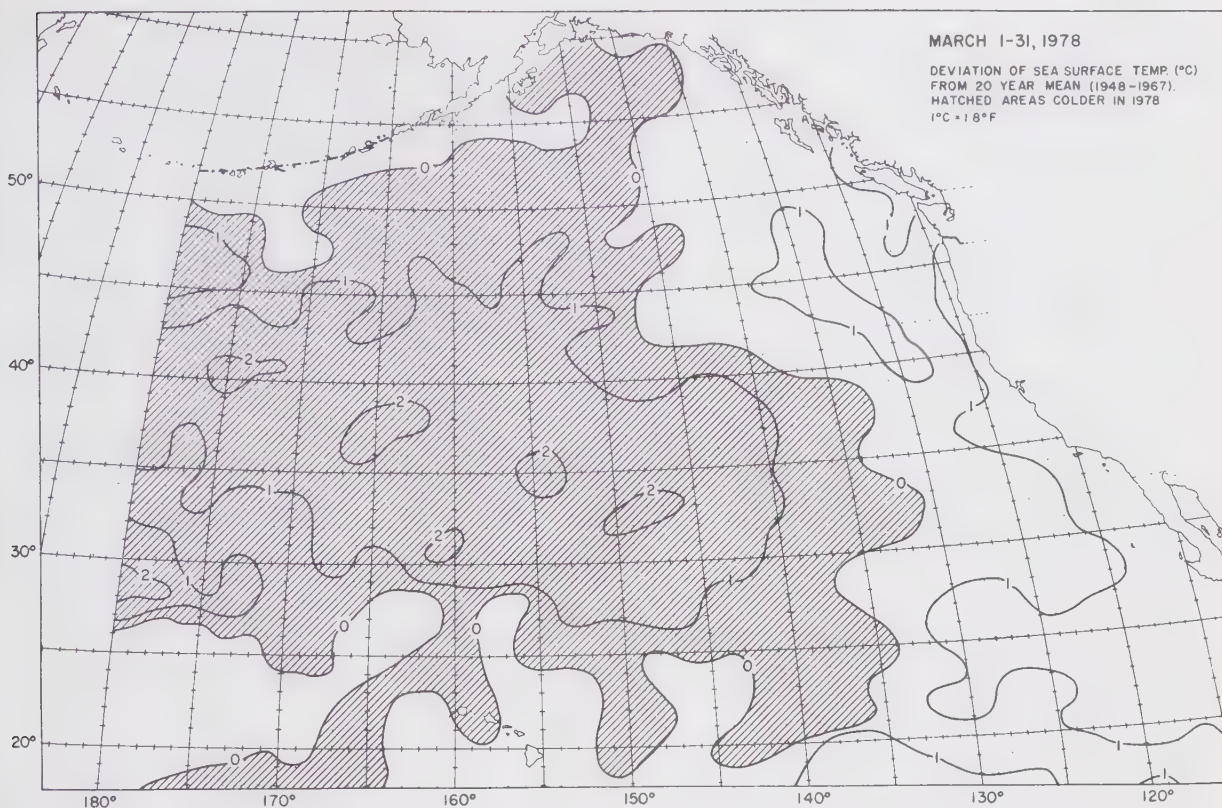


Figure 7.—Anomaly of sea surface temperature (°C) for March 1978 from the 20-year monthly mean (1948-67). Hatched area was colder in 1978 than long-term mean (from *Fishing Information*, March 1978).

the mid-latitude zone where the meridional temperature gradient is greatest to 8°C in the Gulf of Alaska and 5°C in the subtropics. In the coastal region the amplitude of variation is much reduced by upwelling of cool waters during summer (Oregon and south) and slightly reduced by downwelling in winter along the Alaska coast.

Contoured charts of the anomaly of SST (the departure of SST from the 20-year monthly mean) for the eastern North Pacific are published monthly in *Fishing Information*.⁴ In all but 1 of the 15 monthly SST anomaly charts published for 1977 and early 1978, a large body of cooler-than-normal water appeared roughly centered in a

band along lat. 40°N between long. 175°E and 150°W. (The chart showing this feature for March 1978 is reproduced here as Figure 7.) Latitude 40°N is about the axis of the West Wind Drift Current and the latitude of a large north-south gradient in temperature. Eber (1971) described the frequent occurrence of persistent large-scale SST anomalies between lat. 30° and 50°N in the North Pacific Ocean and proposed that they were produced by a quasi-stationary wave pattern in the West Wind Drift Current. A southward displacement of the Current in mid-Pacific and northward displacement east of long. 150°W could have produced, in a gross sense, the negative temperature anomaly pattern found during 1977 and early 1978. The development of this feature had begun during the latter half of 1976, hence it

was a phenomenon having a longer time scale than that of the monthly variations in wind-induced Ekman transport.

Details of the variation of sea surface temperature along the coast are discussed later for individual sections of coastline. In general, however, coastal SST variations were characterized by broad regions of positive anomalies during the early months of both 1977 and 1978. In March 1977 coastal regions were near normal and by April they were cooler than normal. For the remainder of the year the coastal region was generally cooler than normal, especially in November. In December there was a relaxation of the negative anomalies and an excessive warming off Baja California. By January the coastal region from Baja California to southeastern Alaska was

⁴*Fishing Information*, published monthly by Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

again warmer than normal. The positive anomaly grew in magnitude and extent through March 1978 (Fig. 7).

Eastern Bering Sea

The Bering Sea is a deep ocean basin separated from the open North Pacific Ocean by the Aleutian Island Chain. In the eastern portion of the basin there are extensive areas of shallow water supporting abundant fishery resources. The oceanography of the shallow areas is dominated in the winter and spring by the extent and duration of ice cover and in spring and summer by heating and river discharge. Fast moving, intense storms originating in the North Pacific Ocean as well as locally have major effects on ice cover, runoff, and ocean currents.

Oceanographic data from the area are scarce and there are relatively few routine observations of oceanographic conditions due to the remote location and to winter ice cover. Air temperature records at weather stations, river discharge measurements, and scattered observations at a few coastal stations are the only long-term data available.

Ice

The extent of ice cover in winter and the timing of ice breakup in spring are important environmental factors affecting fishes and fisheries in the eastern Bering Sea. Satellite infrared imagery and weekly charts of ice distribution issued by the U.S. Navy and National Environmental Satellite Service (NESS) provide information on ice conditions in the eastern Bering Sea. A graphical representation of the mid-month positions of the ice edge, based on the Navy and NESS data, is shown in Figure 8 for the ice seasons of 1976-77 and 1977-78. For comparison, the position of maximum ice extent during the previous season (1975-76) is also shown on Figure 8. Overall, ice cover was above normal in winter and spring 1977 and normal or even slightly above normal in late fall 1977, but below normal during the winter of 1977-78. Only small amounts of ice remained in embayments on the north side of Bristol Bay in late March. In addition,

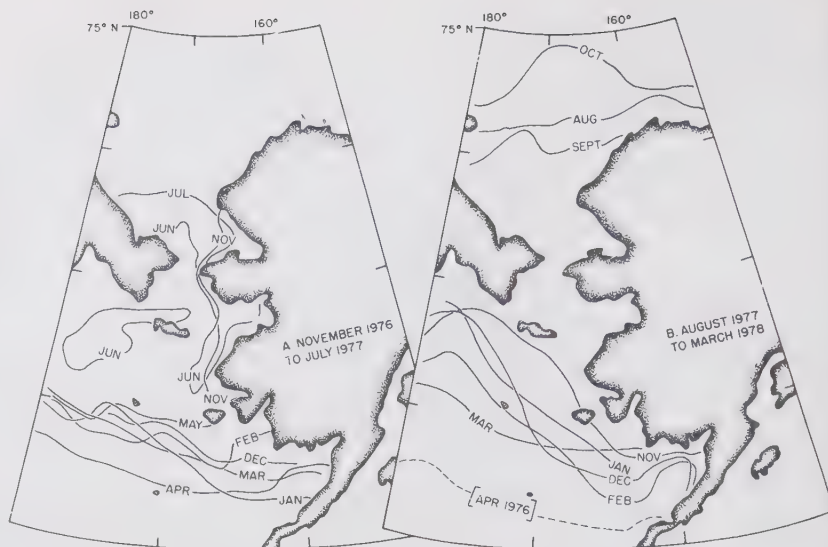


Figure 8.—Mid-month locations of ice front in eastern Bering and Chukchi Seas during November 1976 to March 1978 and, for comparison, April 1976. Plotted from data of the National Environmental Satellite Service and from ice cover analyses from U.S. Navy Fleet Weather Central, Suitland, Md.

the breakup of lake ice in the area is expected to be early.

Temperature

Air temperatures over the eastern Bering Sea during 1977 and early 1978 were generally warmer than normal as a result of southerly winds associated with the persistent high pressure ridges in the upper air circulation. Anomalies of air temperature at St. Paul Island in the Pribilofs were positive in 8 out of 13 months in which data were available in 1977 and early 1978 and ranged up to 4.1°C above normal. Temperatures farther north along the coast at King Salmon, Nome, and Kotzebue also were generally above normal, particularly in early 1977 and early 1978. In January 1977, King Salmon, Nome, and Kotzebue all observed air temperatures 9° to 11°C above normal. This was the warmest January on record at King Salmon and Nome.

Thus 1977 and early 1978 broke a stretch of 6 years (1971-76) in which temperatures in the southeastern Bering Sea were much below normal. Stocks of such marine species as

sockeye salmon and halibut were adversely affected by the cold years (McLain and Favorite, 1976). The warm conditions of 1977-78 should allow more rapid than normal growth rates of salmon and halibut in the Bering Sea and of juvenile salmon in tributary streams and lakes.

The water of the eastern Bering Sea is isothermal during winter with temperatures throughout the water column during winter of -1.8°C under the ice and 1°-3°C just north of the Alaska Peninsula, depending on the southern extent of the ice cover. Warming in spring and summer of the surface layer closely parallels increasing air temperatures, but dilution from ice-melt and rapidly increasing land runoff quickly stabilizes the water column and confines further warming to the upper 20-30 m. Thus, bottom temperatures generally reflect the extent of ice cover until late summer and early fall when horizontal advection and downward diffusion of heat can increase bottom temperatures prior to winter overturn and seasonal ice formation.

In general, bottom temperatures in the eastern Bering Sea were considerably warmer in 1977 than in 1976 (or much of the 1970's). Data from NMFS research surveys⁵ and other vessels indicated that bottom temperatures in the corridor into Bristol Bay north of the Alaska Peninsula were near normal (about 3°C) during late spring and early summer 1977. In spring 1976 temperatures of less than 0°C had occurred and apparently hindered the eastward onshore movement of halibut (Favorite et al., 1977:151⁶).

Runoff

There are six major rivers discharging into the eastern Bering Sea. These rivers and their average annual flows (100,000 cubic meters per second) are: Yukon (17.6), Kuskokwim (4.6), Kvichak (0.4), Kuzitrin (1.3), Wood (0.6), and Nuyakuk (0.6). Although ice jams in spring (not only in the rivers but at the river mouths) influence the freshwater discharge from the extensive snowsheds, ice breakup usually occurs in the low flow lowland rivers (Egegik, Naknek) by mid-April, in the Kuskokwim Bay by 1 May, and the entrance to the Yukon River by early June.⁷ In May, the mean daily discharges of most rivers increase an order of magnitude (e.g., for the Yukon River from about 700 to 17,000 cubic meters per second and for the Kuskokwim River from 300 to 2,800 cubic meters per second); maximum values have been maintained at times until summer.

Although runoff data were only available through September 1977 at the time of this report, generally

normal discharge had occurred in the Yukon River (Fig. 9). However, above normal runoff was apparent for the Nuyakuk River in summer 1977 because local rainfall added to the snowmelt discharge. Reports from field personnel indicate above normal rain, ground water tables, and lake levels in early 1978.

Aleutian Islands to Icy Bay

Flow along the south coast of Alaska and the Alaska Peninsula moves southwestward toward the Aleutian Islands where part of the flow moves northward into the Bering Sea, part continues westward along the Aleutian Chain, and the remainder turns southward and recirculates into the Gulf of Alaska.

Ice

Ice conditions in Prince William Sound and Cook Inlet were mild in both winters 1976-77 and 1977-78 and most bays were ice free by March of each year.

Temperature

Observations at coastal weather stations on the south coast of Alaska

indicate that air temperatures were above normal in early 1977 and early 1978 but were near normal or below normal in mid and late 1977. Air temperatures were up to 3°C above normal at Cold Bay and Kodiak and 1° to 8°C above normal at Homer and Yakutat in January and February of both 1977 and 1978.

Sea surface temperatures⁸ along the coast from the eastern Aleutians to Icy Bay (Fig. 10) normally range from minimum values of 3°-6°C in January to March to maximum values of 9°-14°C in August or September. Winter minima are lowest in the Kodiak Island and Alaska Peninsula areas while summer maxima are greatest off Prince William Sound and to the east.

Throughout the period January 1977 to March 1978 SST's (Fig. 11) were generally higher than normal along the entire coastline from the eastern Aleutian Islands to Icy Bay. Water temperatures 0.5° to 2.0°C higher than normal were common along the coast from Unimak Pass to Cook Inlet during the first half of 1977. During the second half of 1977 and early 1978 SST's returned to near normal although they continued mild. Water 1.0° to 2.4°C cooler than normal occurred off Prince William Sound and Cook Inlet during October 1977 to February 1978 but warmed to above normal in March 1978.

Generally both winters (1976-77 and 1977-78) were unusually warm. The mild winters and related high rainfalls have resulted in good survival of juvenile salmon as indicated by studies of preemergent fry. The warm conditions may advance the herring spawning by 1 or more weeks. Like the southeastern Bering Sea to the north across the Alaska Peninsula, the mild

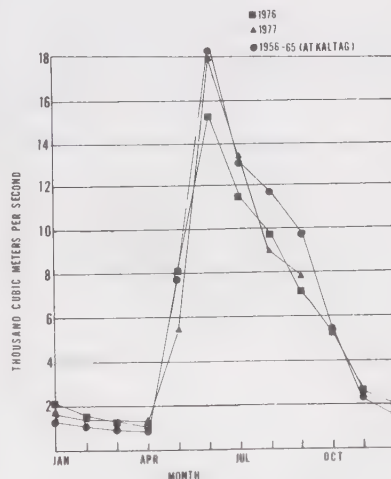


Figure 9.—Discharge of Yukon River at Pilot Station for 1976 and 1977 and 1956-65 long-term mean at Kaltag in thousands of cubic meters per second. Data from U.S. Geological Survey.

⁵Otto, R. S., J. E. Reeves, and J. Burns. 1977. King and Tanner crab research in the eastern Bering Sea, 1977. Unpubl. manuscript. Northwest and Alaska Fisheries Center, NMFS, NOAA, Seattle, WA 98112.

⁶Favorite, F., T. Laevastu, and R. R. Straty. 1977. Oceanography of the northeastern Pacific Ocean and Bering Sea, and relations to various living marine resources. Processed report, 280 p. Northwest and Alaska Fisheries Center, NMFS, NOAA, Seattle, WA 98112.

⁷Seifert, R., and D. Kane. 1977. Effects of seasonability and variability of stream flow on nearshore coastal areas. Unpubl. manuscript. Inst. Water Resour., Univ. Alaska, Fairbanks, AK 99701.

⁸Averages of SST reports were made by 1° squares of latitude and longitude from observations made by passing ships and received by Fleet Numerical Weather Central. Maps of the original data are on file at Pacific Environmental Group, but for brevity only plots of SST by distance along the coast are included in this report. The long term mean values of SST are means for the period 1948-67 of SST observations in Tape Data Family-11, National Climatic Center, Environmental Data Service, NOAA, Asheville, NC 28801.

conditions which had begun in mid-1976 broke a 6-year run of below normal temperatures. This cold period was particularly serious in the Kodiak Island region where air temperature anomalies had been negative during 56 of the 69 months from August 1970 to April 1976 (anomalies were zero or positive in 11 months and data were missing in 2 months). Effects of cold weather had been severe on both salmon and pink shrimp in the Kodiak area.⁹

Runoff

Major rivers in this area and their annual mean discharge (100,000 meters per second) are: the Copper (2.4), Susitna (1.0), and Knik (0.7). Although a qualitative assessment of runoff indicates near normal conditions in 1977, total precipitation in Prince William Sound appeared to be below normal. Light snow pack occurred in 1978 and may result in low stream flows during the early salmon spawning season.

Salinity

Information on the distribution of surface salinity in Gulf of Alaska coastal waters during summer 1977 is available from a joint U.S.-Poland fishery oceanography survey conducted by the *Profesor Siedlecki* (Fig. 12). Immediately evident is the extensive dilution in the area of the Copper River. Another striking feature is the advection of water of less than 32‰ salinity over the continental slope at the head of the Gulf, well seaward of the inshore dilution caused by runoff from the Copper River. This apparent bifurcation of northwestward coastal flow, which has not been detected or reported before, may possibly influence the transport of ichthyoplankton, particularly halibut larvae, as well as the seaward migration path of salmon smolts from southeastern Alaska, British Columbia, Washington, and Oregon areas.

⁹Jerry McCrary, Regional Research Supervisor, Alaska Department of Fish and Game, Kodiak, AK 99615, pers. commun.

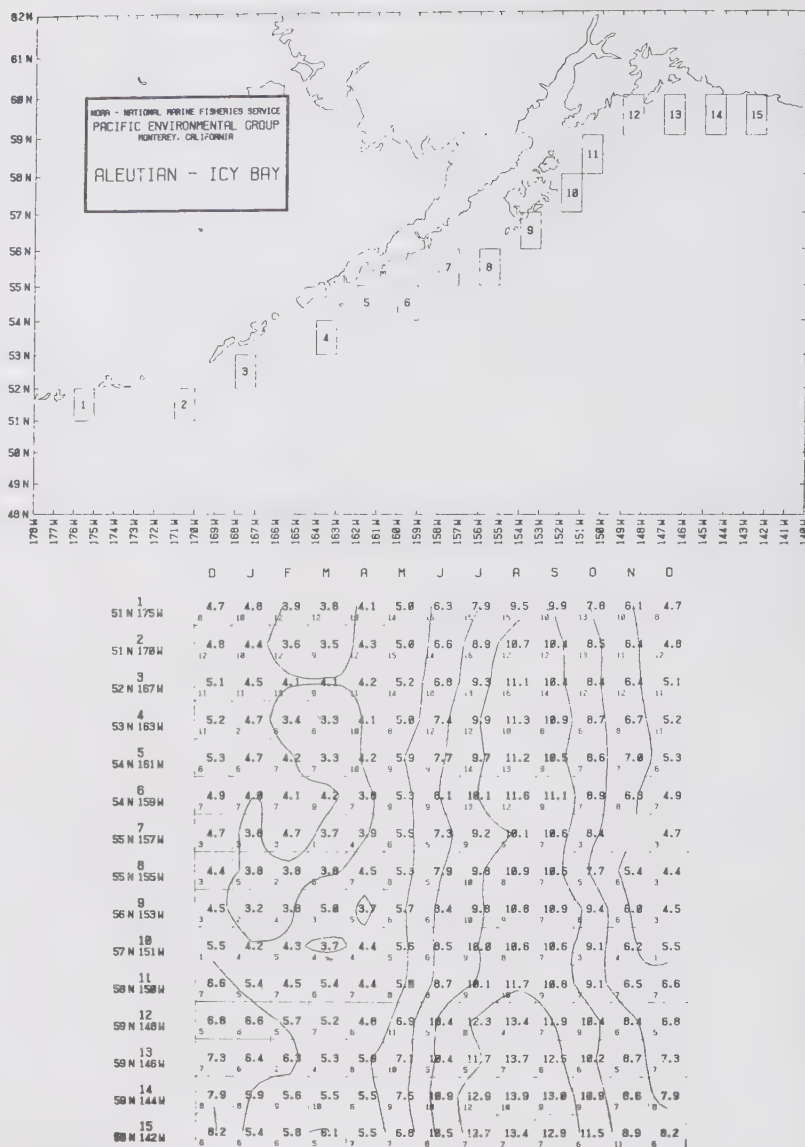


Figure 10.—Location of 1° squares (upper) and 1948-67 long-term mean (lower) sea surface temperature in °C by 1° squares from Aleutian Islands to Icy Bay. Number of years of data available for each location is shown below SST value. Contour interval is 2.0°C.

Icy Bay to Strait of Juan De Fuca

The region of the northwest coast off southeastern Alaska and British Columbia is oceanographically the region where the West Wind Drift Current splits as it flows eastward toward the coast. Part flows north into the Gulf of

Alaska and the remainder flows south as the California Current.

Temperature

Sea surface temperatures along the coast of southeastern Alaska and British Columbia follow somewhat the

same trend as those to the westward described earlier (Fig. 13). Minimum temperatures of 4° to 7°C occur in March or April and maximum temperatures of 13° to 16°C occur in August.

During 1977 and early 1978, water temperatures off the northern portion of southeastern Alaska (Fig. 14) were similar to those to the west off Prince William Sound with warm water during January to July 1977 and generally cool water until February 1978. Off southern southeastern

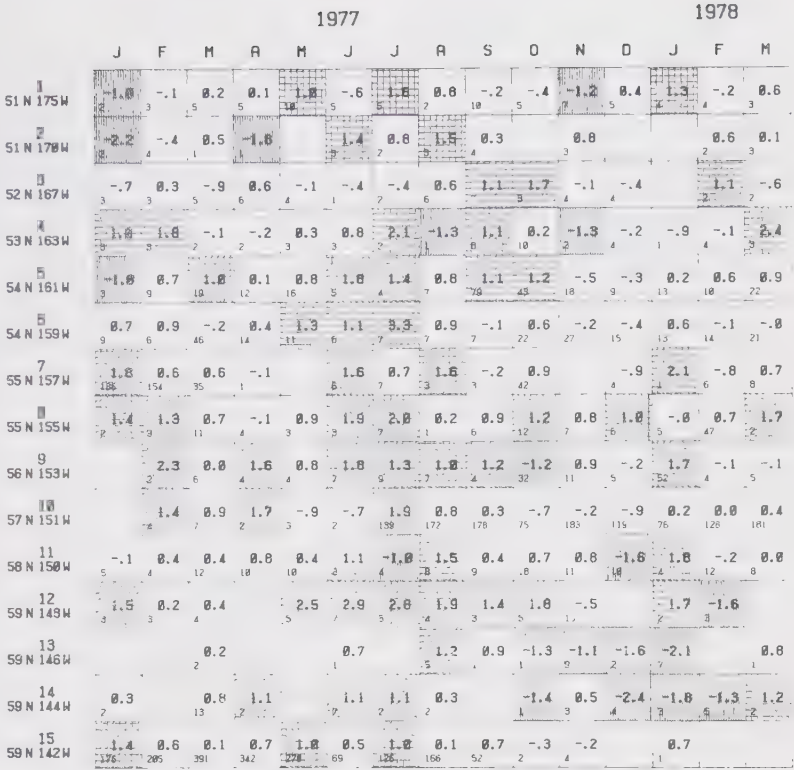


Figure 11.—Anomalies of monthly mean sea surface temperature in °C from 1948-67 mean and numbers of observations by 1° squares from Aleutian Islands to Icy Bay for period January 1977 to March 1978. Squares are hatched for anomalies of +1.0°C or above and shaded for anomalies of -1.0°C or below.

Figure 12.—Surface salinity in parts per thousand, July 1977. Observations made by the research vessel *Professor Siedlecki*.

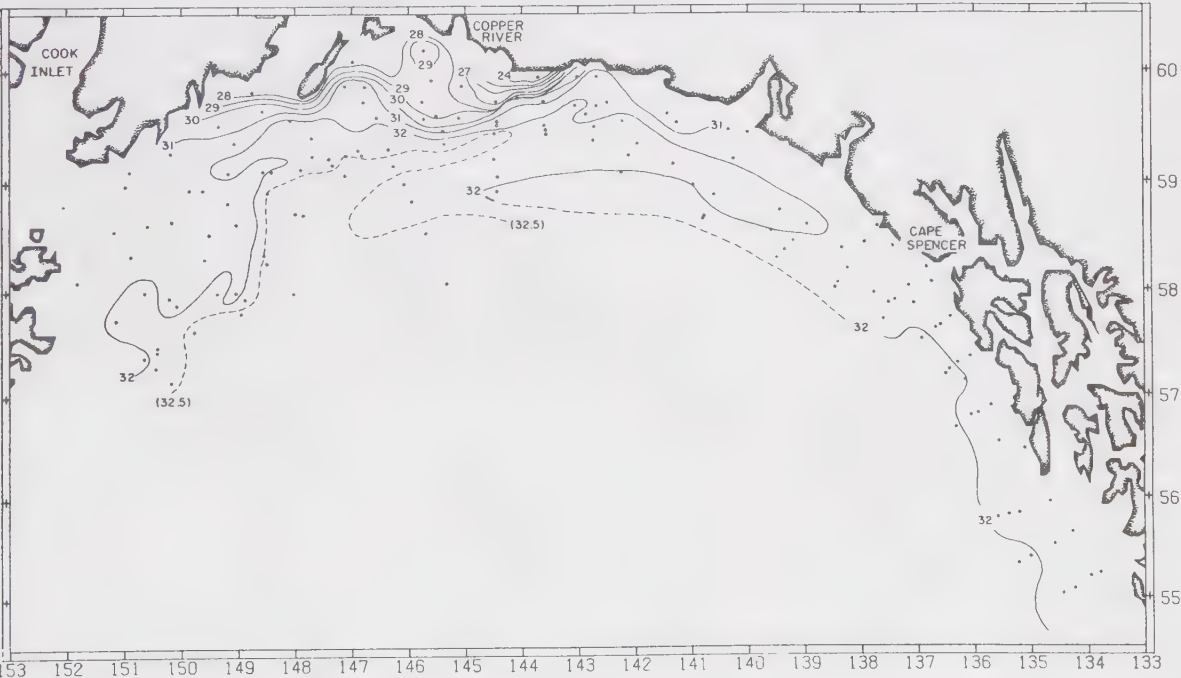


Table 1.—Representative winter sea surface temperatures ($^{\circ}\text{C}$) at Sitka and Auke Bay, Alaska, 1976 to 1978.¹

Area	Jan.	Feb.	Mar.	Remarks
Sitka				
1976	4.5	3.7	4.1	Cool
1977	6.4	6.1	5.7	Exceptionally warm
1978	4.2	4.6	4.8	Mild, warm
Auke Bay				
1976	2.6	2.6	2.4	Cold
1977	4.0	4.8	5.7	Exceptionally warm
1978	3.3	3.1	3.3	Mild, warm

¹Based on data compiled by B. L. Wing, Northwest and Alaska Fisheries Center Auke Bay Laboratory, National Marine Fisheries Service, NOAA, Auke Bay, AK 99821

Alaska and British Columbia, SST anomalies were more variable. Warmer than normal water occurred along the coast in January to March 1977 and again in March 1978. Cooler than normal water was prevalent off Vancouver Island during April to August.

Monthly mean coastal SSTs are available from coastal stations at Sitka and Auke Bay, Alaska, and indicate that winter conditions were 1.5° to 3°C warmer in 1977 than 1976 and up to 0.9°C warmer in 1978 than in 1976 (Table 1).

Data on SST fluctuations along the British Columbia coast are available from four lighthouse stations in exposed locations which make daily observations.¹⁰ Monthly means of these data show that temperatures at all four stations during the first half of 1977 were 0.5° to 1.5°C warmer than normal with greatest positive anomalies off the northern British Columbia coast. During the second half of 1977 water temperatures were near normal. In early 1978 water temperatures again became warmer than normal (0.5° to 1.0°C above normal) with greatest positive anomalies off central British Columbia.

Scattered subsurface temperature measurements by expendable bathythermographs taken during the latter

¹⁰Monthly means of daily surface temperature and salinity observations at Langara Island, Cape St. James, Kains Island, and Amphitrite Point were kindly furnished by L. F. Giovando, Pacific Environmental Institute, Environment Canada, West Vancouver, B.C. V7V 1N6.

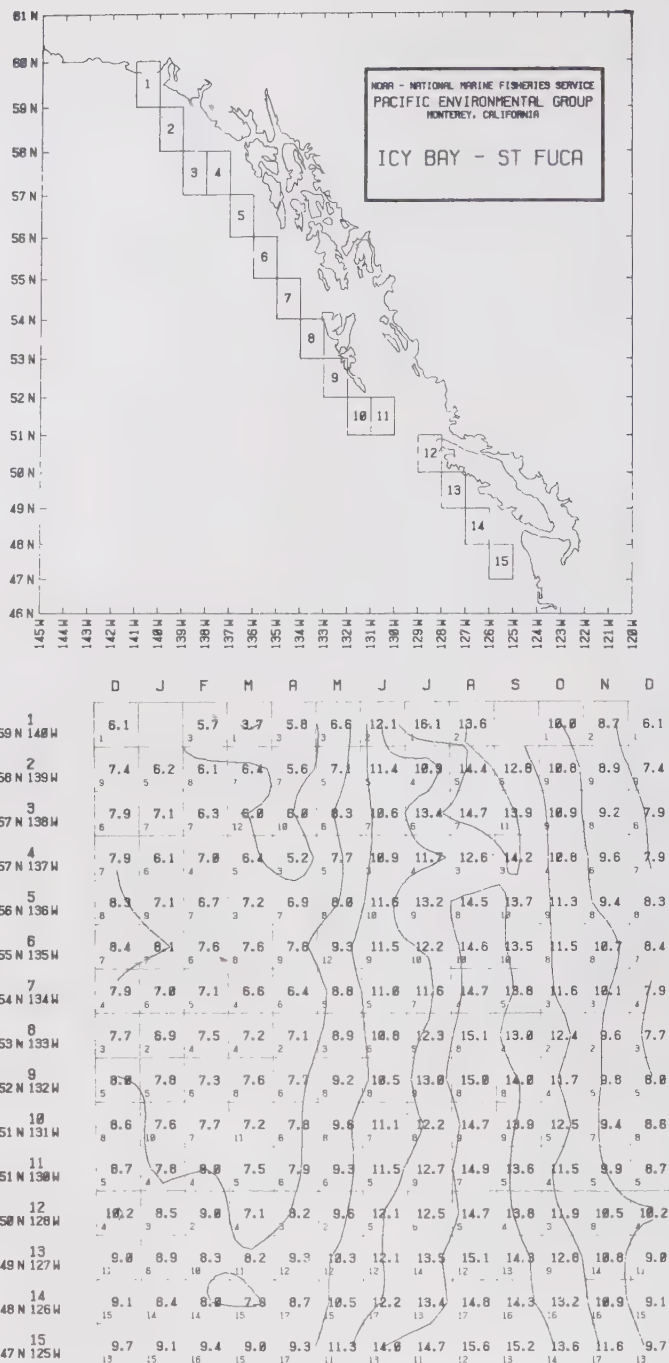


Figure 13.—Location of 1° squares (upper) and 1948-67 long-term mean (lower) sea surface temperature in $^{\circ}\text{C}$ by 1° squares from Icy Bay to Strait of Juan de Fuca. Number of years of data available for each location shown below SST value. Contour interval is 2.0°C .

part of March 1978 off the southern coast of Vancouver Island indicate the presence of anomalously warm water (9.5° – 10°C) throughout the water column.¹¹

Salinity

Measurements of surface salinity are also made daily at the British Columbia lighthouses (footnote 10). These data indicate that water salinities off the British Columbia coast were often 0.3 to 1.0‰ above normal during 1977. Data from early 1978 are available for only one station (Langara Island) and they indicate that salinities were 0.5 to 1.0‰ below normal.

Strait of Juan De Fuca to Gulf of California

Off the west coast of the United States, relatively cool and low salinity waters are transported southward by the California Current. The Current contains meandering streams of flow and eddies but in long term averages the Current appears as a slow, broad flow. These waters are separated from the warmer, more saline North Pacific Central waters to the west by the Transition Zone—a region of ocean fronts. The northward flowing California Undercurrent lies inshore of the California Current, immediately adjacent to the coast and is seasonally variable. From Oregon southward to Baja California, prevailing northwest winds in summer cause upwelling of deeper, nutrient rich waters which support biological productivity. Ingraham and Love (1978) presented detailed observations of water temperature, salinity, and concentration of dissolved oxygen made in the summer of 1977 over the continental shelf along the coast by the Polish research vessel *Profesor Seidlecki*. The data show many details of the spatial distribution of properties but, unfortunately, comparable data are not available for other years.

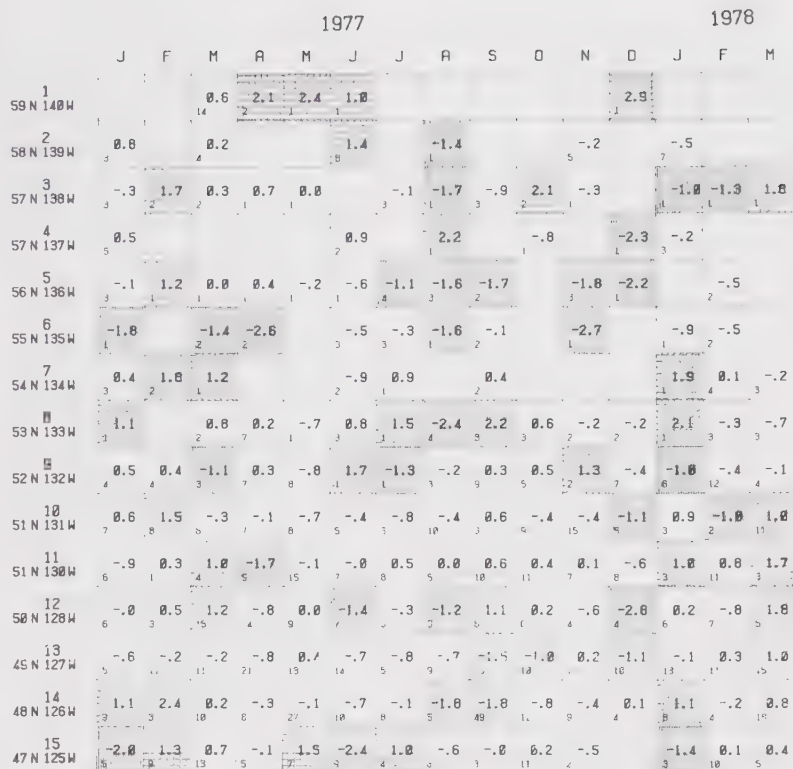


Figure 14.—Anomalies of monthly mean sea surface temperature in $^{\circ}\text{C}$ from 1948–67 mean and numbers of observations by 1° squares from Icy Bay to Strait of Juan de Fuca for period January 1977 to March 1978. Squares are hatched for anomalies of $+1^{\circ}\text{C}$ or above and shaded for anomalies of -1°C or below.

California Current and Transition Zone

The structure of the California Current and Transition Zone¹² regions has been monitored routinely since 1966 by merchant ships operating between San Francisco and Honolulu. These ships make observations of surface and subsurface temperature and surface salinity at about 120-km intervals along the track on a twice monthly schedule. Along the ship transit lane the surface water temperatures and salinities had been near normal during the winter of 1975–76 (Saur, 1978). During the winter of

1976–77 the salinities were 0.2 to 0.5‰ lower than the previous winter between long. 129° and 146°W and surface temperatures were similar to those of the previous winter (Saur and McLain, In press). During the winter of 1977–78 salinities in the same region were lower yet, 0.4–0.5‰ below average, while the corresponding temperatures had decreased on the order of 1.5°C . One possible explanation for these observations is that there was a significant increase in the advection of cool, low-salinity subarctic waters southward and into the California Current. Computations of Ekman transport (Fig. 4) suggest an increase in the West Wind Drift Current in both winters. Another possible cause is a significant increase in precipitation. During these winters

¹¹A. J. Dodimead, Pacific Environmental Institute, Environment Canada, West Vancouver, B.C. V7V 1N6, pers. commun.

¹²Material for this section was developed by J. F. T. Saur, Scripps Institution of Oceanography, La Jolla, CA 92038.

there were large regions of increased southerly winds, indicative of storms and the transport of tropical, high humidity air northward. While both factors (increased advection and precipitation) were likely operative, there were some important differences in each year. During the winter of 1976-77 the winds with an anomalous southern component occurred west of long. 130°W (Fig. 2, lower). Excess local precipitation was then probably a principal cause of the observed low salinities as there is not the requisite time lag for advection to significantly alter the salinity. In the following winter (1977-78) the anomalous southern wind component occurred nearer the coast (east of long. 135°-140°W, Fig. 3, lower) where records of low salinity and high rainfall suggest excess precipitation. Farther offshore the decrease in temperature and salinity suggest that increased advection from more northerly sources was important.

The spring and early summer migration of albacore into the U.S. west coast fishery has been shown to be associated with the Transition Zone and with individual fronts within it (Laurs and Lynn, 1977). The Transition Zone is bounded by strong horizontal gradients of temperature and salinity, the subarctic and subtropical ocean fronts. The degree of development of these ocean fronts appears to affect the path of migration of albacore, their aggregation in offshore areas, and perhaps the timing of their movement into traditional nearshore fishing grounds.

Surveys of the oceanographic character of the fronts have been made annually in recent years. Such a survey was made in June 1977¹³ in the region of the Transition Zone through which the albacore migrate shoreward. The survey found only remnants of the ocean fronts where in other years there had been clearly defined features. Drifter buoys were deployed in the region (lat. 33°N, long. 137°W) and

monitored daily in subsequent months. While the drifting buoys retained their drogues, they moved in circuitous paths. The buoy tracks and the lack of frontal development suggest considerable ocean surface mixing.

The structure of the ocean fronts in the Transition Zone as observed from the merchant ships between San Francisco and Honolulu has been published monthly in *Fishing Information* (footnote 4) since 1972. In March 1977 there appeared to be a well defined subtropical front. In the following months a broad region of temperature inversions occurred without a strong subtropical front. This may be indicative of the mixing found by the June oceanographic survey. In September and October the subtropical front reappeared and was strongly developed. (The surface salinity, which is important in the identification of ocean fronts, was unfortunately not available for many of the transects.) By March 1978 a typical situation prevailed; both fronts were of average intensity.

Temperature

As was noted for the British Columbia coast, sea surface temperatures off Washington and Oregon (Fig. 15) are minimum in March and maximum in August. Off southern Oregon and northern California the normal seasonal warming in summer is depressed by upwelling of cold waters and summer mean temperatures do not reach 14°C, whereas 15°C temperatures are observed to both the north and south. Off central California seasonal heating again becomes dominant and surface temperatures reach summer maxima of over 16°C. The peaks are delayed a month or so, however, from those to the north with minima occurring in March or April and maxima in September.

During January and February 1977 SST's off the west coast (Fig. 16) were generally above normal (up to +2°C anomalies). A strong pulse of upwelling in March (Fig. 5) caused anomalous cooling and by April SST's were below normal along almost the entire stretch of coast with anomalies more

negative than -1.0°C off central California. In May upwelling was weak and SST's rose anomalously. In June, upwelling increased again and temperatures were again below normal. Except for an area of warmer than normal water off northern California in August, SST's remained below normal through November while upwelling remained strong. Temperatures in December were generally above normal. During January through March 1978 water temperatures were consistently above normal (with anomalies of over +2.0°C common) along almost the entire stretch of coast in association with very weak upwelling and, in some instances, downwelling.

Sea surface temperatures from Point Conception southward to the Gulf of California (Fig. 17) show a regular seasonal warming and cooling cycle with minima in March to May and maxima in August or September. During January and February 1977 SST's along the coast (Fig. 18) were almost uniformly 1.5° to 2.5°C above normal as a result of calm, clear weather under the persistent high pressure system which prevailed along the coast. Due to the strong upwelling pulse in March, SST's returned to near normal values and remained near normal through July. A pulse of upwelling in August reduced SST's to below normal but conditions returned to near normal in September and October. Anomalous warming began in October and November and by December SST's were again almost uniformly above normal. Warmer than normal temperatures persisted through March 1978 when anomalies above +2°C were common off northern Baja California in March in association with weak upwelling.

Upwelling

Bakun and Parrish¹⁴ have recomputed the indices of intensity of coastal

¹³Lynn, R. J. Unpublished cruise report, Cruise 111, RV *David Starr Jordan*, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

¹⁴Reported in the Monthly Report for March 1978, Southwest Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

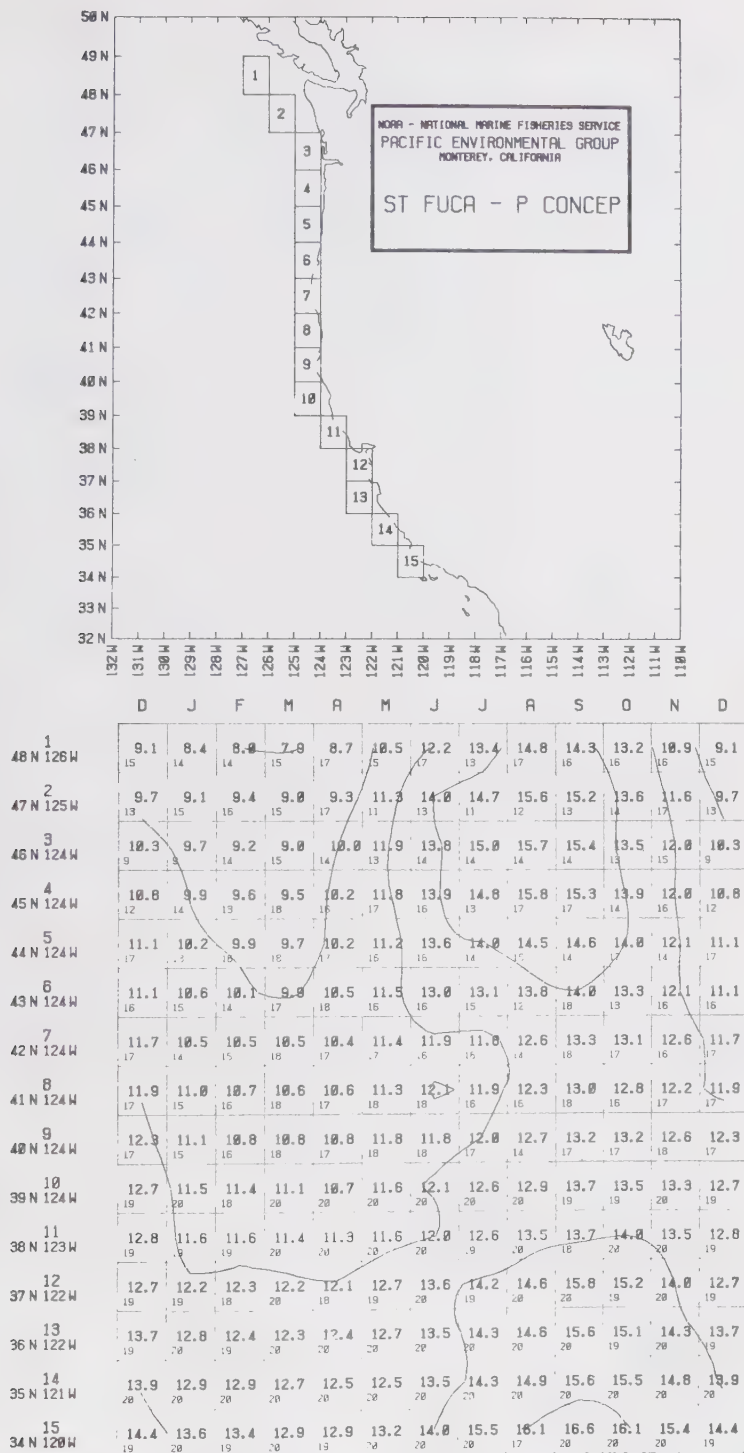


Figure 15.—Location of 1° squares (upper) and 1948-67 long-term mean (lower) sea surface temperature in °C by 1° squares from Strait of Juan de Fuca to Point Conception. Number of years of data available for each location shown below SST value. Contour interval is 2.0°C.

upwelling, described earlier, at 6-hourly intervals for the winters of 1976-77 and 1977-78. They showed that the patterns of upwelling were very different during the two periods. Off California the relatively strong upwelling in the winter of 1976-77 was a relaxed, low-energy situation under the persistent high pressure system that prevailed over California at that time. In contrast the winter of 1977-78 was marked by intense, highly fluctuating upwelling and downwelling episodes as storms moved onto the coast. In monthly averages these episodes appeared as weak upwelling (or downwelling).

The biological effects of these two patterns of upwelling would be quite different. The slack conditions from November to February of 1976-77 should have subjected organisms to less than normal levels of onshore and offshore excursions of surface waters, to reduced turbulent mixing, and to reduced dispersion of planktonic aggregations. During 1977-78, however, strong pulses of wind caused onshore-offshore excursions which should have caused strong turbulent mixing, destroying patch structure of plankton. Smith and Lasker (1978) suggested that changes in concentrations of plankton due to upwelling changes may be an important factor in survival of larval anchovies.

Runoff

The Columbia River, whose seaward discharge is second only to the Yukon River, and the accumulated flow from the Fraser River and the Puget Sound Basin that discharges through the Strait of Juan de Fuca, are nearly equivalent. However, mixing and stirring processes in the Strait diminish the salinity differences between inshore and coastal waters, whereas marked salinity gradients occur at the edges of the Columbia River plume. Columbia River runoff data for January to September 1977 (Fig. 19) indicate a 50 percent reduction from the same period in 1976, reflecting the west coast drought. Perhaps more significant is the absence of a peak discharge in May or June

1977. During this annual, critical runoff period, flow was only a third of normal conditions and half those of 1976. The absence of this annual pulse of freshwater could have a variety of effects on salmon in the river and on coastal marine organisms.

Salinity

Lower than normal surface salinities were observed by the merchant ships in the California Current between San Francisco and Honolulu as has been mentioned. Low salinities were also observed on research cruises of the California Cooperative Oceanic Fisheries Investigations in early 1978. The cruises covered roughly the area within 450 km of the coastline from central California to Baja California. The series of surveys, in December 1977 and January, March, and April 1978, revealed an increasing and expanding salt deficit in the surface layer. The freshened waters are attributed to unusually high local precipitation which reflected the heavy rains observed at coastal stations. The excess rainfall, computed as that amount of freshwater required to produce the salinity anomaly, was approximately 0.5 to 1 m over the 5 months, December 1977–April 1978. This amount is twice the excess rainfall recorded at San Diego (0.22 m) and Santa Barbara (0.57 m) for the same period and 2-3 times the estimated annual average rainfall. The anomalously low salinities extended well into the pycnocline. The low salinity values at depth may be due to increased advection of low salinity water from the north.

Eastern Tropical Pacific Conditions

Oceanographic conditions in the eastern tropical Pacific (ETP) are influenced by the Equatorial current systems and their variations.¹⁵ The

¹⁵Much of the material of this section was prepared by Forrest Miller, Inter-American Tropical Tuna Commission, La Jolla, CA 92037. It is based on material developed for *Fishing Information* and the reader is referred to that publication for charts of monthly sea surface temperature (SST) and anomaly of SST from a long-term mean.

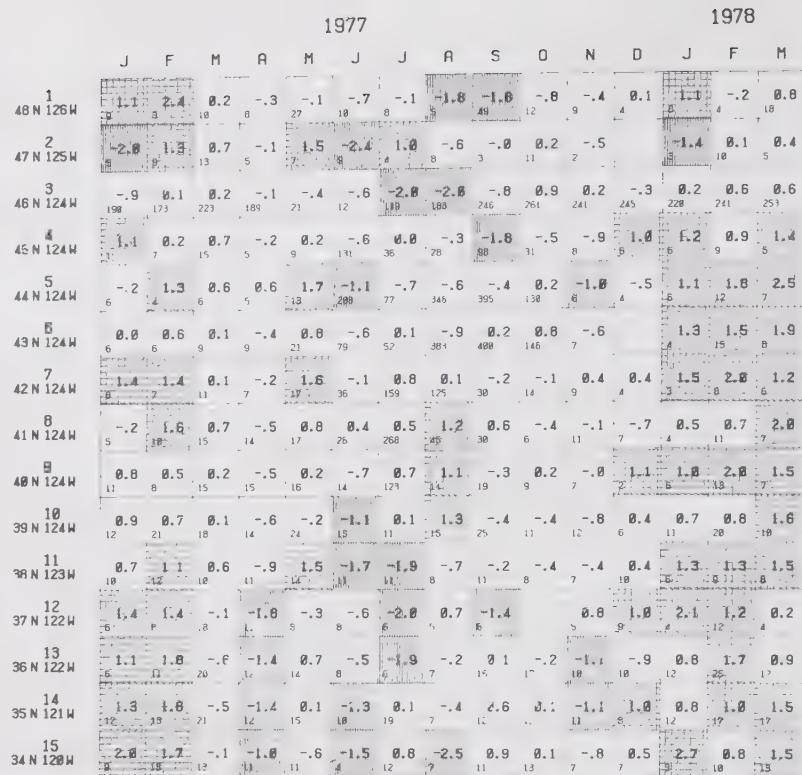


Figure 16.—Anomalies of monthly mean sea surface temperature in °C from 1948-67 mean and numbers of observations by 1° squares from Strait of Juan de Fuca to Point Conception for the period January 1977 to March 1978. Squares are hatched for anomalies of 1°C or above and shaded for anomalies of -1°C or below.

trade winds of the equatorial regions drive the westward flowing North and South Equatorial Currents.

The North and South Equatorial Countercurrents flow eastward. Variations in these currents occur and major changes, known as El Niño events, transport unusually large amounts of warm, saline waters towards the coast. Such events are related to fluctuations in the strength and position of the trade winds over large areas of the tropical Pacific. Quinn (1976, 1978, in press) has described relations of El Niño conditions in the ETP to the Southern Oscillation—a variation of atmospheric pressure across the tropical Pacific Ocean. Upwelling occurs off the west coasts of Peru and Ecuador and along a broad band westward along the Equator as a result of divergence

caused by the trade winds. Upwelling is strongest during August and September.

Variations in oceanographic conditions in the ETP affect the fishery resources of the area in various ways. A major El Niño event occurred in 1972 and was followed by a serious decline in production of anchoveta off Peru. The exact mechanism of the decline is still in question but it no doubt involved a combination of heavy fishing pressure and environmental change. Tunas are mobile, highly migratory animals and are related to their environment in complex ways. Changes in the distribution and availability of tunas are related to variations in SST, thermocline depth, and other oceanographic conditions while variations in skipjack tuna

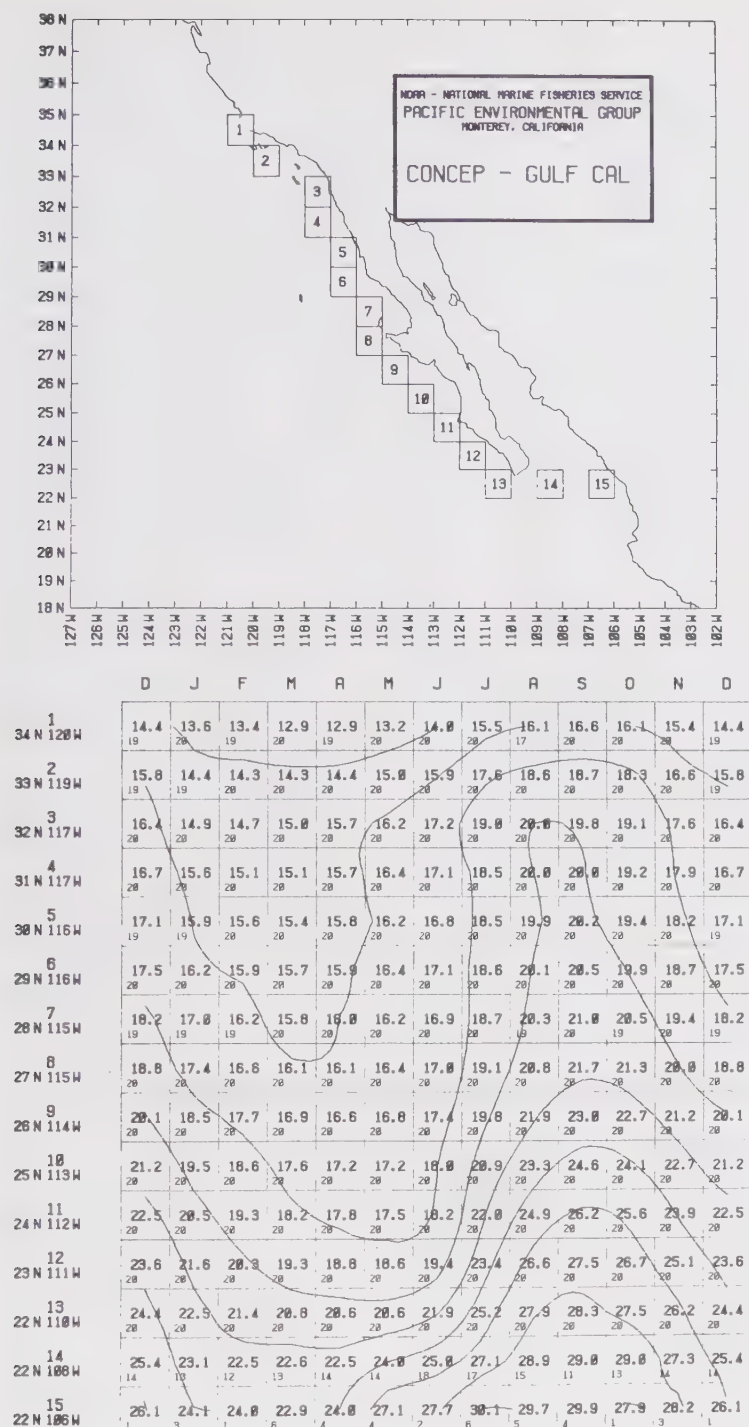


Figure 17.—Location of 1° squares (upper) and 1948-67 long-term mean (lower) sea surface temperature in °C by 1° squares from Point Conception to Gulf of California. Number of years of data available for each location shown below SST value. Contour interval is 2.0°C.

abundance have been correlated with the Southern Oscillation.

Sea Surface Temperature

Fluctuations of oceanographic conditions in the ETP are commonly monitored from patterns of SST. Such patterns can be characterized as complex patterns of ocean fronts bordering on large warm and cool water areas. Fairly regular seasonal changes occur in the locations and intensities of these frontal boundaries and associated SST patterns. The seasonal pattern is modified in El Niño years when SST's are unusually high over most of the ETP and ocean fronts along the Equator are weak. Frequently, during 1 or more years preceding an El Niño, SST's are abnormally low over large areas of the tropics, especially along the Equator as a result of strong trade winds and strong equatorial upwelling.

A moderately intense El Niño had occurred in 1976 (Quinn, in press) with associated positive SST anomalies reaching a maximum in December 1976. During January to March 1977 (Fig. 20), SST's remained above normal over most of the ETP. As was seen in Figure 18, SST's along the coast of Baja California were more than 1°C above normal. Along the southwest coast of Central America and over most of the ETP north of lat. 5°N, SST's were within 0.5°C of normal. Along the Equator east of long. 150°W and off Peru, there were several areas where SST's were more than 1°C above normal from the warming during the 1976 El Niño although these areas diminished rapidly in size during January. The Gulfs of Tehuantepec and Panama and waters off the south coast of Peru (south of lat. 15°S) all experienced SST's which were more than 1°C below normal during the first quarter due to strong wind mixing.

During April to June a distinct shift from warm to cool conditions took place over most of the coastal areas off the west coasts of Mexico (Fig. 18) and also off Central and South America with SST's reaching as much as 1°C below normal off Ecuador. Along the Equator from lat. 5°N to 5°S upwelling reduced SST's to 0.5° to 1°C below

normal in April. During May the area of negative SST anomalies (more than 1°C below normal) expanded westward from the Galapagos Islands-Ecuador region. This pattern of SST anomalies—below normal temperatures off Central and South America and along the Equator and near normal temperatures elsewhere in the ETP—persisted through October. Maximum negative anomalies (as much as -1.5°C below normal) due to upwelling along the Equator occurred in September. During 1977 the Southern Hemisphere subtropical high pressure system (normally centered near lat. 30°S, long. 90°W) was not in its normal position and surface pressures were frequently below normal. As a result, the southeast trade winds and upwelling were weaker than normal along the coast of South America and over the equatorial central Pacific.

During July to December, SSTs in the Northern Hemisphere and west of long. 120°W warmed faster than normal and the eastern part of the ETP north of the Equator warmed more slowly than normal. Negative anomalies along the Central American coast (east of long. 100°W and north of lat. 5°N) occurred during this period and were associated with increases in tropical storm activity which increased markedly in July. A band of negative SST anomalies offshore of the coast of Central America and Mexico occurred in areas of heavy wind mixing in the paths of tropical storms which developed from July to October 1977.

Apart from seasonal changes the SST anomalies during October to December did not markedly change from earlier conditions. Tropical storm activity in the ETP from Costa Rica to Baja California continued through October leaving a broad zone of deeply mixed tropical water and scattered areas with negative anomalies (greater than 1°C below normal) where storms intensified most often. West of long. 120°W and south of lat. 20°N SSTs were more than 1°C above normal due to below normal cloud cover and light trade winds. By November the areas of large positive anomalies were reduced

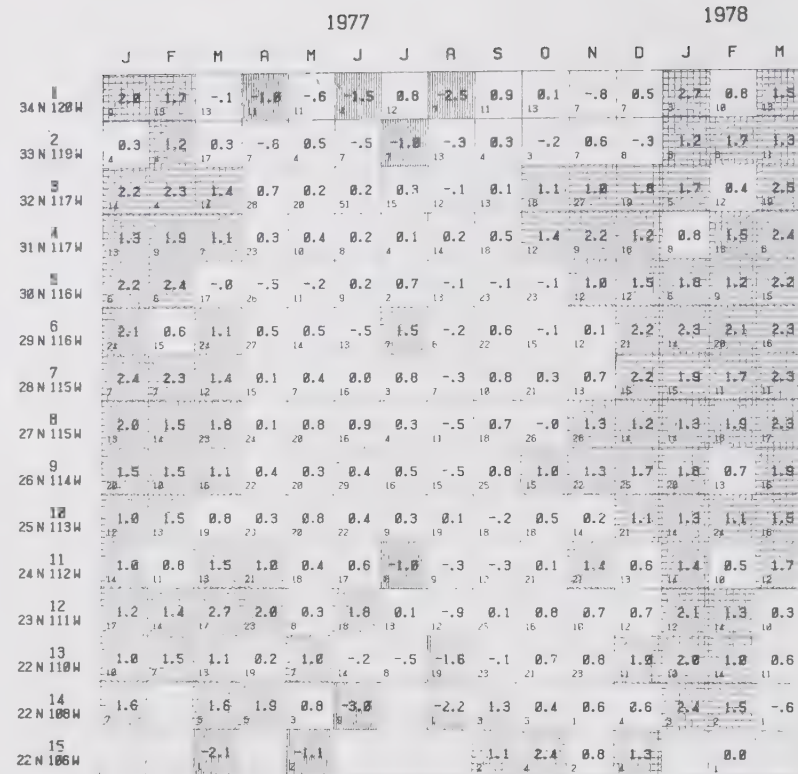


Figure 18.—Anomalies of monthly mean sea surface temperature in °C from 1948-67 mean and numbers of observations by 1° squares from Point Conception to Gulf of California for period January 1977 to March 1978. Squares are hatched for anomalies of +1°C or above and shaded for anomalies of -1°C or below.

in size. In the Southern Hemisphere SSTs remained slightly above normal with scattered areas of positive anomalies greater than 1°C until the end of the year. However, by December SSTs in the area west of long. 85°W from lat. 5° to 30°S, which had been above normal since May 1975, were beginning to return to normal. Along the coast of South America and along the Equator (lat. 5°N to 5°S), SSTs were, on an average, slightly below normal most of the time with an occasional positive anomaly extending into the equatorial region from the trade wind zones of both hemispheres.

During January 1978 temperatures throughout the ETP were near normal with the exceptions of warmer than normal water off Baja California due to the weak upwelling there and cooler than normal water off Peru and west of

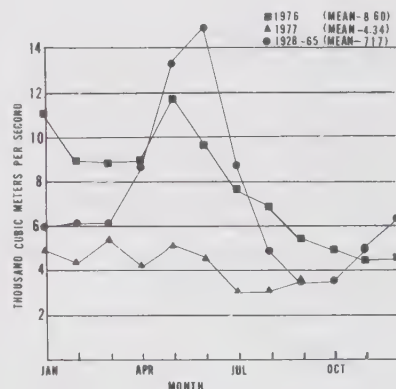


Figure 19.—Discharge of Columbia River near Astoria for 1976 and 1977 and 1928-65 long-term mean in thousands of cubic meters per second. Data from U.S. Geological Survey.

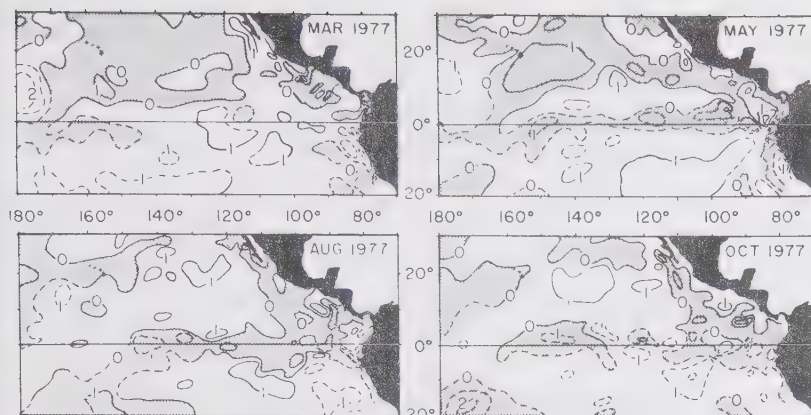


Figure 20.—Departure of sea surface temperature (in °C) from long term monthly averages in the eastern tropical Pacific Ocean for 4 months of 1977. Shaded areas are below average. (Adapted from *Fishing Information*.)

the Galapagos Islands due to strong upwelling. Below normal water temperatures continued to occur in the Gulfs of Tehuantepec and Panama due to wind mixing. This pattern continued during February and March although the cooler than normal water west of the Galapagos Islands was not present in March.

Tuna Fishing Conditions

From January through April 1977 the catches of yellowfin tuna east of long. 100°W were the lowest for that period in 18 years. The low catches were due in part to a tie-up (during April and May) of much of the U.S. tuna fleet in response to porpoise fishing regulations. Another factor affecting fishing in the ETP was high winds which prevailed all winter in and around the Gulfs of Tehuantepec and Panama and off the west coasts of Nicaragua and Costa Rica. The frequent outbreaks of high winds and rough seas kept the tuna fleet on the move in the ETP looking for suitable fishing areas. During May and June there was considerable tuna fishing activity along the southwest coast of Baja California near a strong north-south SST gradient. By May above normal SST's and related light winds and seas attracted large numbers of tuna boats to an area west of long.

110°W and south of lat. 10°N where fishing was good. However, tuna fishermen east of long. 110°W between lat. 5° and 15°N reported poor fishing from April to mid-June due to an extensive area of high SST's (29°C and greater) that persisted throughout the second quarter.

During most of the period from July to December, tuna fishing on the "Local Banks" off the west coast of Baja California was better than usual because of the above normal SST's and to the strong north-south gradient of SST south of lat. 25°N. South of Mexico and west of Central America fishing activity was considerably reduced from July to October because of the development of frequent and intense tropical storms. Wind mixing of the surface layers in the path of storms made the location of fish and purse seining difficult from lat. 10°N to 10°S and along the coast to long. 115°W. During the last half of 1977 many tuna boats moved south to an area south of lat. 5°N between long. 120° and 100°W where fishing weather was better than farther north and SST's were in the range 25° to 28°C. This fishing area was probably south of the north Equatorial Counter Current and north of the equatorial ocean front where forage may aggregate and attract large schools of tuna.

Acknowledgments

Data for this report were provided by Fleet Numerical Weather Central, Monterey, Calif. Andrew Bakun made the computations of Ekman transport and upwelling index. Jim Renner contributed plots of atmospheric pressure and winds. Jim Ingraham compiled material on conditions in the Gulf of Alaska as did J.F.T. Saur for the California Current. Forrest Miller contributed material on oceanographic and fishery conditions in the eastern tropical Pacific. Elizabeth Haynes, R. Michael Laurs, and Robert Pedrick reviewed the manuscript and suggested improvements.

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Smith, P. E., and R. Lasker. 1978. Position of larval fish in an ecosystem. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 173:77-84.

Appendix I

Principal Sources of Data and Information Used:

Atlantic Environmental Group, National Marine Fisheries Service, NOAA, Narragansett, RI 02882. Surface and subsurface temperature data from monthly XBT transects off New York and southern New England. Unpublished reports by staff oceanographers.

Environment Canada, Pacific Environmental Institute, West Vancouver, B.C. V7V 1N6. Monthly means of daily surface temperature and salinity observations from Canadian lighthouse stations. Scattered subsurface temperature observations in Canadian waters.

Fishery Engineering Laboratory, National Marine Fisheries Service, NOAA, Bay St. Louis, MS 39529. Unpublished data on Mississippi River flow and positions of the East

Gulf loop current.

National Climatic Center, Environmental Data Service, NOAA, Asheville, NC 28801. Local climatological data: monthly summaries of daily and 3-hourly observations at selected weather stations.

National Environmental Satellite Service, NOAA, Washington, DC 20233. Weekly satellite-observed Gulf Stream analysis charts. Miami SSFS Analysis charts produced weekly.

Northeast Fisheries Center, National Marine Fisheries Service, NOAA, Woods Hole, MA 02543. Surface and subsurface temperature data and surface salinity data from monthly transects across the Gulf of Maine. Unpublished reports by staff scientists.

Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93940. Sea surface temperature anomaly charts: monthly by 1° square. Computer processed transects of expendable bathythermograph and salinity observations from ships of opportunity between San Francisco, Calif., and Honolulu, Hawaii. Space-time plots of sea surface temperature anomalies for selected 1° squares along the Atlantic coast. Computations of surface layer (Ekman) transport and listouts of data: monthly on alternate 5° or every 3° grid.

U.S. Army Corps of Engineers Regional Office, New Orleans, La. Mississippi River discharge data.

Appendix II

Publications scanned for environmental or fisheries information:

Mariners Weather Log, (bi-monthly), Environmental Data Service, NOAA, Washington, DC 20235.

Monthly Weather Review, American Meteorological Society, Boston, MA 02108.

National Fisherman, (monthly newspaper), Camden, ME 04843.

Fishing Information, (monthly), Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

U.S. Geological Survey Periodic summaries of streamflow data in various regions in the Atlantic and Gulf coastal areas, issued on varying time schedules by Regional Offices (advance release of data may be arranged by personal communication).

U.S. Naval Oceanographic Office, Washington, D.C. Experimental ocean frontal analysis charts produced weekly from satellite infrared imagery and expendable bathythermograph observations.

Virginia Institute of Marine Sciences, Gloucester Point, Va. Press releases regarding fisheries status.

Determining the Best Trade-Off Between Expected Economic Return and the Risk of Undesirable Events When Managing a Randomly Varying Population

ROY MENDELSSOHN

Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, USA

MENDELSSOHN, R. 1979. Determining the best trade-off between expected economic return and the risk of undesirable events when managing a randomly varying population. *J. Fish. Res. Board Can.* 36: 939-947.

Conditions are given that imply there exist policies that "minimize risk" of undesirable events for stochastic harvesting models. It is shown that for many problems, either such a policy will not exist, or else it is an "extreme" policy that is equally undesirable. Techniques are given to systematically trade-off decreases in the long-run expected return with decreases in the long-run risk. Several numerical examples are given for models of salmon runs, when both population-based risks and harvest-based risks are considered.

Key words: Markov decision processes, risk, salmon management, Pareto optimal policies, trade-off curves, linear programming

MENDELSSOHN, R. 1979. Determining the best trade-off between expected economic return and the risk of undesirable events when managing a randomly varying population. *J. Fish. Res. Board Can.* 36: 939-947.

L'auteur expose les conditions qui sous-entendent l'existence de politiques aptes à minimiser le risque d'événements indésirables dans l'élaboration de modèles stochastiques de récolte. Il démontre que, pour plusieurs problèmes, une telle politique n'existe pas, ou encore on a une politique «extrême», également indésirable. Il décrit des méthodes selon lesquelles une diminution des gains anticipés à long terme peut être systématiquement échangée contre une diminution du risque à long terme. Il donne plusieurs exemples pour modèles de remontées de saumons, dans lesquels sont considérés risques inhérents à la population et risques inhérents à la récolte.

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I. Introduction

AN important consideration in managing ecosystems or wildlife populations is the avoidance of undesirable occurrences, either to the populations themselves, or to the economic agents acting on them. This might mean minimizing the chance that a population becomes too small, or minimizing environmental damage, or perhaps minimizing the chance that the economic return is too small. Such ideas of minimum risk are inherent in such legal concepts as optimal sustainable population (OSP), required for the management of marine mammals in the U.S., or in management under extended jurisdiction, where both the health of the stocks and the health of the industry are vital concerns.

Underlying these concerns is some notion of risk or uncertainty in our management measures. This can arise from two causes. The first cause of risk is risk in the system itself. For example, if oceanographic systems affect fish stocks, we cannot with certainty predict the stock size next year, but only predict with given probability. The second cause of risk is uncertainty

about these probabilities. This second cause presumably would diminish as more and more observations are made, and our knowledge about the system increases.

In this paper we are concerned with the first cause of risk — inherent uncertainty in the system. The results and techniques can be extended to include the second case also (for extensions in related areas see Rieder (1975) or van Hee (1978)). Risk enters our decisionmaking process in three ways. Firstly, in constructing the probabilities of the occurrence of given events. Secondly, in the decisionmaker's attitude towards risk, e.g. how much of a gamble will be tolerated to obtain a possibly higher total return. And finally, the policy selected can be analyzed for the degree of risk that it entails.

In this paper, an effort is made to make precise the rather vague decisionmaking goal of "minimizing risk" in a dynamic context. We will see initially that intuitively appealing definitions lead to policies that are not reflective of the true complexity of the problem (section III). As an alternative, acceptable trade-offs between low risk in the long run and high expected economic return must be found. To this end, the concept of a "Pareto optimal solution" is introduced, and

its uses in evaluating trade-off curves are explored (section IV). Several numerical examples of the techniques of section IV are presented in section V.

II. The Model

We restrict attention to single species Markov models without age structure. A Markov model has transition probabilities (e.g. the probability of a given population size next period) that depend only on the present population size and the present harvesting decision. However, it is possible, by increasing the size of the "state" to include sufficient statistics of the past history, to have Markov models that include time lags and other more complex features. Many of the results extend to models with these complexities, as well as models with age structure or multispecies models; however, the more complex models neither help to further illustrate the limitations of a notion like "minimize risk," nor do they make any clearer the alternative methods proposed. Hence only simple models will be explored. At the beginning of each period t , the population size is "observed" to be x_t . During period t , z_t of the population is removed, leaving a population size of $y_t = x_t - z_t$ at the end of period t . The population size at the beginning of period $t + 1$ is assumed to be a random function of y_t , that is

$$(2.1) \quad x_{t+1} = D_t s[y_t]; \quad D_t \geq 0 \quad \text{with probability}$$

where $D_1, D_2, \dots$ are independent, identically distributed random variables distributed as the generic variable D .

A one-period decision rule in period t is any rule that tells us that if x_t is the observed state at the start of period t , then take action y_t (e.g. harvest z_t), and does so for all possible values of x_t . A policy π is a sequence of decision rules; that is, an n -period policy π_n would be defined as

$$\pi_n = \{\delta_1, \delta_2, \dots, \delta_n\}.$$

Consider the following two problems:

$$(2.2a) \quad (i) \text{ for fixed } \omega, \text{ "minimize" } Pr\{x_t \leq \omega\} \quad \text{for all } t$$

$$(2.2b) \quad (ii) \text{ for fixed } \eta, \text{ "minimize" } Pr\{z_t \leq \eta\} \quad \text{for all } t.$$

This implies finding some infinite horizon policy π^* such that this probability is always smallest.

To make this more precise, we need to define the notion of *stochastic dominance* (Lehmann 1966; Keilson 1974; Barlow and Proschan 1975; O'Brien 1975). For two random variables x and y defined on a common probability space Ω , let F be the distribution function of x and G the distribution function of y . Then x is said to be stochastically dominant over y , written $x \geq y$ if and only if

$$F(x(\omega)) \leq G(y(\omega)) \quad \text{for all } \omega \in \Omega$$

that is the random variable y has a distribution function

that always has more total accumulated probability at lower values. It is easy to see that if $x \geq y$, then

$$Pr\{x \leq \omega\} \leq Pr\{y \leq \omega\}$$

for all ω .

In comparing two Markov chains $\{x_n, n \in N_0\}$ and $\{y_n, n \in N_0\}$ defined on a common probability space, $\{x_n\}$ is said to be stochastically dominant over $\{y_n\}$ if

ST.

$$x_n \geq y_n \quad \text{for all } n \in N_0.$$

This implies (2.2a) or (2.2b); as we shall see, stochastic dominance is a useful concept.

III. Policies That are Stochastic Dominant

Our first theorem can be motivated by considering the one-period problem: for a given x_1 , choose a y_1 such that

ST.

$$D_1 s[y_1] \geq D_1 s[x_1] \quad \text{for } 0 \leq y \leq x_1$$

where $s[\cdot]$ is assumed to be unimodal.

Now

$$Pr\{D_1 s[y_1] \leq \omega\} = Pr\left\{D_1 \leq \frac{\omega}{s[y_1]}\right\}.$$

Consider the policy δ_1^* defined by

$$\delta_1^* = \text{minimum } \{y_{\max}, x_1\}$$

where $y_{\max}$ is the argument where $s[\cdot]$ achieves its mode. Then, for any other feasible decision rule δ_1

$$s\{\delta_1^*(x_1)\} \geq s\{\delta_1(x_1)\} \quad \text{implies}$$

$$\frac{\omega}{s\{\delta_1^*(x_1)\}} \leq \frac{\omega}{s\{\delta_1(x_1)\}} \quad \text{implies}$$

$$Pr\left\{D_1 \leq \frac{\omega}{s\{\delta_1^*(x_1)\}}\right\} \leq Pr\left\{D_1 \leq \frac{\omega}{s\{\delta_1(x_1)\}}\right\}$$

which is the desired result.

Theorem 3.1 formalizes this result; the proof is given in the appendix, as are all the proofs in this paper.

Theorem 3.1 — In (2.1), assume $s[\cdot]$ is unimodal and obtains its mode at $y_{\max}$. Define the policy $\pi^* = \{\delta_1^*, \delta_2^*, \dots\}$ where

$$\delta_t^* = \text{minimum } \{x_t, y_{\max}\}.$$

Let $\{x_n^{\pi^*}\}$ be the Markov chain that arises from following π^* , and $\{x_n^{\pi}\}$ be the Markov chain that arises from following any other feasible policy π . Then

ST.

$$x_n^{\pi^*} \geq x_n^{\pi} \quad \text{for all } n. \quad \square$$

The assumption that $s[\cdot]$ is unimodal is weak, as most standard production models satisfy this assumption. The specific form $x_{t+1} = D_t s[y_t]$ is also common; see for example the models of salmon runs in Bristol Bay developed by Mathews (1967).

It is worth comparing the policy that arises from theorem 3.1, with the policy that

$$(3.1) \quad \begin{aligned} &\text{maximizes} \quad E \left\{ \sum_{t=1}^{\infty} \alpha^{t-1} p \cdot (x_t - y_t) \right\} \\ &\text{s.t.} \quad x_{t+1} = D_t s[y_t]; \quad 0 \leq y_t \leq x_t \end{aligned}$$

and $s[\cdot]$ restricted as before. It has been shown by Mendelsohn and Sobel (unpublished data) that the solution of (3.1) is of the form

$$\bar{\delta}_t = \text{minimum} \{x_t, y^*\}$$

where $0 \leq y^* \leq y_{\max}$.

As an example of the difference between these two policies, consider the following model for salmon in the Wood River postulated by Mathews (1967):

$$x_{t+1} = (e^d) 4.077 y_t \exp \{-0.800 y_t\}$$

where d is distributed as $N(0, 0.2098)$. Solved on a 51-point grid, $y^* = 0.700$ (Mendelsohn 1978b) when $\alpha = 0.97$. On this same grid, $y_{\max} = 1.26$ which is close to the true $y_{\max}$ of 1.25 (the grid points are in units of 10^6 fish).

Two measures of interest will be examined. The first is the mean per period harvest under the two policies. The second is the long-run probability of being in any state. (This is the vector ϕ , where

$$\phi(x) = \sum_{j \in X} \phi(j) P_{jx}^{\pi}.)$$

Following $\{\delta_t^*\}$ yields a mean per period harvest of 0.916727×10^6 fish, following $\{\bar{\delta}_t\}$ yields a mean per period harvest of 1.188993×10^6 fish.

Figure 1 shows the distribution function of the stationary probabilities arising from the two policies. The policy $\bar{\delta}$ which maximizes the long-run expected harvest has a greater average harvest compared with δ^* of 272 263 fish, and with a lower variance between harvest amounts. $\bar{\delta}$ also has a zero harvest only 3.28% of the years, while the minimum risk policy δ^* does not harvest 19.67% of the time.

Conversely, the minimum risk policy almost halves the probability of being in the low population sizes of 420 000–840 000 fish, from 7.4% of the time to 4.1% of the time.

Clearly these two policies are the two extremes. A natural question is how to find policies, if any exist, that greatly increase the expected total discounted harvest, at only a small increase in risk.

Theorem 3.1 can be generalized slightly by assuming that $x_{t+1} = s[y_t, D_t]$. In this model the random variable need not act multiplicatively as before.

Theorem 3.2 — If, except for the zero state, every $x \in X$ can be reached with positive probability from every other $x \in X$, and (i) if there exists a δ^* such that

$$\text{ST.} \quad s[\delta^*(x_1), D_1] \geq s[\delta(x_1), D_1]$$

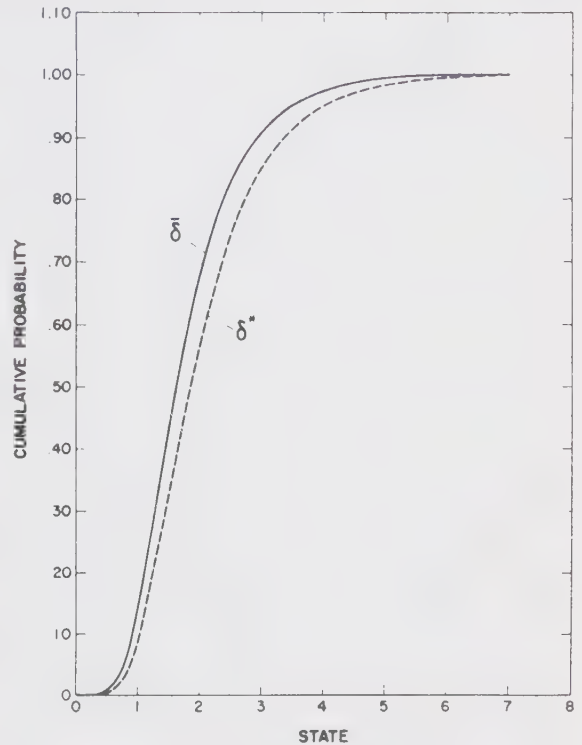


FIG. 1. Cumulative stationary probability distribution ($Pr [x \leq \epsilon]$) when following policies δ^* and $\bar{\delta}$. The minimum risk policy δ^* has a mean harvest of 0.917×10^6 , and a variance of 0.894×10^6 . The maximal expected total (discounted) harvest policy $\bar{\delta}$ has a mean harvest of 1.189×10^6 , and a variance of 0.787×10^6 .

for all feasible decision rules δ and all $x_1 \in X$; then

$$\pi^* = (\delta^*, \delta^*, \dots)$$

is a stochastically dominant policy. (ii) if no such δ^* exists, then there does not exist a policy that is stochastically dominant. $\square$

The advantage of theorem 3.2 is that only a one-period problem need be solved. Either that solution is the long-term solution also, or if no solution exists for this "static" problem, then no solution exists for the larger problem.

I have not been able to find any policies that are stochastically dominant when the criteria is (2.2b); nor have I been able to prove that such a policy doesn't exist. However, I conjecture the following:

Conjecture 3.1 — There is no policy π^* , such that the Markov chain of the amount harvested following π^* , $\{z_n^{\pi^*}, n \in N_0\}$, compared with the Markov chain $\{z_n^{\pi}, n \in N_0\}$ that arises from following policy π , satisfies

$$\text{ST.} \quad z_n^{\pi^*} \geq z_n^{\pi} \quad \text{for all } n$$

for every possible feasible π . $\square$

It is worth reviewing where we are. We have found a stochastically dominant policy under certain assumptions. This was found to produce a solution that greatly reduces the economic return from the harvest (in fact, if $s[\cdot]$ is nondecreasing, then theorem 3.1 states that the risk is minimized by *not harvesting at all*). Also, for certain other models, it has been either proven or conjectured that *there does not exist a policy that minimizes the risk of an undesirable event*. Finally, a numerical example has led us to speculate that a large gain in economic return can be obtained by incurring only a small increase in the risk.

IV. Pareto Optimal Policies

In most decisionmaking situations, the decision-maker usually is faced with not one, but rather a myriad of conflicting objectives. However, intuitively we often feel that even in this situation, there is a "best" policy in the sense that this "best" policy most fairly balances the different objectives. To examine all the trade-offs possible could be even more confusing than enlightening for the decisionmaker. It would be desirable to reduce the set of policies that need to be evaluated in examining these trade-offs.

One such set of policies are policies that are "Pareto optimal," or more precisely, whose expected returns are Pareto optimal. If there are two objectives, Pareto optimal policies have an intuitive explanation: A policy is Pareto optimal if there is no other feasible policy that does at least as well in any one of the objectives, and strictly better in the other objective.

To describe this more formally, let Π be the set of all possible policies; let $v^\pi = (v_1^\pi, v_2^\pi, \dots, v_k^\pi)$ be the vector value of the k objectives $v_1, v_2, \dots, v_k$. Let V be the set of all possible v^π for $\pi \in \Pi$. Then a policy $\pi^* \in \Pi$ is said to be Pareto optimal if there does not exist some other policy $\pi \in \Pi$ such that

$$v^\pi \geq v^{\pi^*}.$$

(When comparing two k -vectors $x = (x_1, \dots, x_k)$ and $y = (y_1, \dots, y_k)$, $x = y$ implies $x_i = y_i$, $i = 1, \dots, k$; $x \geq y$ implies $x_i \geq y_i$, $i = 1, \dots, k$; $x \geq y$ implies $x \geq y$ but $x \neq y$; and $x > y$ implies $x_i > y_i$, $i = 1, \dots, k$.)

For the problems of this section, we will restrict Π to the class of stationary policies, that is, policies that follow the same one-period decision rule in each period. There is a body of literature that shows that for our models, when maximizing economic return over a very long planning horizon, this is without loss of generality.

In section III, we were concerned with a class of problem that can be viewed as a multiobjective problem: Any policy is evaluated in terms of the expected (discounted) value of the harvest from that policy; it is also evaluated in terms of the degree of long-run risk of an undesirable event that occurs from

following this policy. Our goal now is to find the class of Pareto optimal policies between these two objectives, and to find the trade-off curve on this set of policies, rather than trying to strictly optimize.

To accomplish this, assume problem (3.1) has been discretized on a set of states $X_1 = (x_1, x_2, \dots, x_k)$ and a set of feasible decisions from each $x \in X_1$ is given by $Y(x) = \{y | 0 \leq y \leq x; y \in X_1\}$. If it is desired to maximize the long-run average harvest, or more formally

$$E \left\{ \lim_{T \rightarrow \infty} \left(\frac{1}{T} \right) \left[\sum_{t=1}^T (x_t - y_t) \right] \right\}$$

subject to the transition and harvest constraints, then this is equivalent to solving the following linear programming problem (DeGhellinck 1960; Manne 1960):

$$\begin{aligned} & \text{maximize} \quad \sum_{x \in X_1} \sum_{y \in Y(x)} u_x^y G_x^y \\ (4.1) \quad & \text{subject to} \\ & \sum_{y \in Y(x)} u_x^y - \sum_{j \in X_1} \sum_{y \in Y(j)} u_j^y P_{jx}^y = 0 \quad x \in \{X_1/1\} \\ & \sum_{x \in X_1} \sum_{y \in Y(x)} u_x^y = 1 \\ & u_x^y \geq 0 \quad \text{for all } x \in X_1, y \in Y(x) \end{aligned}$$

where G_x^y is the one-period return of observing x and harvesting to y , P_{jx}^y is the probability of going from state j to state x when action y is taken, and $\{X_1/1\}$ implies the set of states X_1 less some arbitrary base state. That is, if there are k states, there will be $k-1$ of these constraints.

At an optimal solution, $\bar{u}_x^y > 0$ if and only if choosing action y from state x is an optimal decision. Also, the optimal variables $\bar{u}_x^y$ have the interpretation of the probability of being in state x and taking decision y . Suppose it is desired to limit the long-run probability that the process is in states contained in some subset X_2 of X_1 . This can be included into (4.1) by amending the following constraint:

$$(4.2) \quad \sum_{x \in X_1} \sum_{y \in Y(x)} u_x^y \leq \omega.$$

Similarly, if it is desired to limit the probability that the harvest is less than a given amount, let Z_1 be the set of (x, y) pairs that harvest the fixed amount or less. Then amend the constraint

$$(4.3) \quad \sum_{(x,y) \in Z_1} u_x^y \leq \eta.$$

The advantage of this approach is that linear programming allows for parametric analysis of the right-hand sides of the constraints. Thus, it is simple to start off with ω (resp. η) equal to one, that is, the unconstrained or maximum average return problem, and parameterize it to zero, or the minimum long-run risk problem.

If instead it is desired to maximize the expected

total discounted return, then again, after discretizing the problem, a solution can be found by solving the following linear programming problem (d'Epenoux 1963)

$$\begin{aligned}
 & \text{maximize } \sum_{x \in X_1} \sum_{y \in Y(x)} u_x^y G_x^y \\
 (4.4) \quad & \text{subject to} \\
 & \sum_{y \in Y(x)} u_x^y - \sum_{j \in X_1} \sum_{y \in Y(j)} u_j^y \alpha P_{jx}^y = v_x \quad x \in X_1 \\
 & u_x^y \geq 0 \quad \text{for all } x \in X_1 \\
 & y \in Y(x)
 \end{aligned}$$

where α is the discount factor, and the v_x are chosen so that $v_x / \sum_i v_i$ is the initial probability of being in state x .

Recently Sobel (unpublished data) has shown at an optimal solution to (4.4) that

$$\frac{(1 - \alpha) \bar{u}_x^y}{\sum_i v_i} = \text{the normalized discounted fraction of years that state } x \text{ is entered and action } y \text{ is taken.}$$

Note that this is different from the interpretation of the optimal variables in the average return problem, in that here the normalized sum of presence or absence of being in state x and taking action y is discounted, so that near-future behavior is more important than long-run behavior.

Constraints on these probabilities can be amended to (4.4) in a similar manner as probabilistic constraints we amended to (4.3).

Three caveats should be noted carefully. It is always advisable to initially have ω or η identically one and parameterize to zero. This is because at zero the problem may be infeasible, that is, no policy can achieve this constraint. To parameterize an *LP* solution, it is necessary to have an initial feasible solution.

Secondly, a randomized policy may become optimal. A randomized policy is a policy that instead of choosing only one action from each state, chooses one out of several actions from each state by a "lottery" with a given distribution. While this is of some theoretic importance, most policymakers today would not recommend that we manage our resources by tossing dice. However, if only one constraint is amended to (4.2), then Kushner (1971) shows that at most one state will have a randomized decision, and this will involve a "lottery" between at most two actions feasible from that state.

Thirdly, Mendelsohn (1978a) has shown that the size of the grid chosen and the procedure used to discretize the original problem can greatly affect the final values of $\bar{u}_x^y$ for a given problem, as well as the estimates of the stationary distribution $\phi(x)$. Numerical experiments in that paper show that the choice of grid can increase our estimated risk by 3–5 times. Thus it is possible to artificially create a critical trade-off that

does not exist in the original, continuous state space problem.

V. Numerical Examples

To see how these techniques work in practice, consider again the model developed by Mathews (1967) for salmon runs in the Wood River:

$$x_{t+1} = (e^d) 4.077 y_t \exp \{-0.800 y_t\}$$

where d is distributed as $N(0, 0.6768)$.

This is discretized on the following 16-point grid $X_1 = (0, 0.467, 0.933, 1.400, 1.867, 2.333, 2.800, 3.267, 4.200, 4.667, 5.133, 5.600, 6.067, 6.533, 7.000)$

in units of 10^6 fish. Numerical experiments suggest that for real stability in terms of caveat three a 51-point grid should be used. However, this 16-point grid produces an *LP* with 136 variables and 17 constraints; the 51-point grid produces an *LP* with 1326 variables and 52 constraints, a very large problem for illustrative purposes. For management purposes, the larger grid size should be used. The return function of interest is (3.1), and (4.4) rather than (4.1) is analyzed. The reason is that while on a 51-point grid, the optimal policy never goes to state zero, it is easy to demonstrate that on the 16-point grid every policy ultimately is absorbed in the zero state. The discounted problem therefore takes into consideration shorter-run behavior, or conversely, the time to absorption.

The optimal policy for (3.1) for this problem is a base stock policy given by

$$y_t = \text{minimum } \{x_t, 0.933\}.$$

The following constraints were added to (4.4), one at a time:

$$(i) \quad X_2 = \{x \in X_1 : x \leq 0.467\}; v_x = 1 \quad \text{for all } x \in X$$

$$\sum_{x \in X_2} \sum_{y \in Y(x)} \frac{0.03}{16} u_x^y \leq \omega$$

$$(ii) \quad X_2 = \{x \in X_1 : x \leq 0.467\}; v_0 = 0; v_x = \frac{1}{15}$$

otherwise

$$\sum_{x \in X_2} \sum_{y \in Y(x)} (0.03) u_x^y \leq \omega$$

$$(iii) \quad X_2 = \{x \in X_1 : x \leq 0.933\}; v_x = 1 \quad \text{for all } x \in X$$

$$\sum_{x \in X_2} \sum_{y \in Y(x)} \frac{0.03}{16} u_x^y \leq \omega$$

$$(iv) \quad Z_1 = \{(x, y) : x - y \leq 0.467\}; v_0 = 0, v_x = \frac{1}{15}$$

otherwise

$$\sum_{(x,y) \in Z_1} (0.03) u_x^y \leq \eta.$$

The results are summarized in Table 1. For population based probabilistic constraints, an optimal policy moves from a base stock policy of 0.933 to a base stock policy of 1.400, which on the 16-point grid is the optimal minimum risk policy. While any of the

TABLE 1. Bounds on discounted fraction of years $x_t \leq 0.467$, $x_t \leq 0.933$, and $z_t \leq 0.467$.

Total fraction of years, ω	Change in policy		$\frac{(1 - \alpha)}{\sum_t v(i)}$ (value)	
	State	Action		
<i>Bounds on discounted fraction of years $x_t \leq 0.467$</i>				
0.08836	Base stock at	0.933	656.721	1.2314
0.08836	1.867	1.400	656.721	1.2314
0.08735	6.533	1.400	611.634	1.1468
0.08733	3.267	1.400	610.725	1.1451
0.08702	4.667	1.400	596.745	1.1189
0.08696	1.400	1.400	593.696	1.1132
0.08608	4.200	1.400	554.016	1.0401
0.08596	2.333	1.400	548.917	1.0292
0.08518	2.800	1.400	513.729	0.9632
0.08466	7.000	1.400	490.039	0.9188
0.08464	3.733	1.400	489.073	0.9170
0.08444	5.133	1.400	480.126	0.9002
0.08439	6.533	1.400	478.026	0.8963
0.08437	5.600	1.400	477.267	0.8949
0.08434	No change		475.864	
<0.08434	Infeasible			

Initial distribution $v(i) = 1$ for all states i

<i>Bounds on discounted fraction of years $x_t \leq 0.933$</i>				
0.02758	Base stock at	0.933	43.7814	
0.02758	1.867	1.400	43.7814	
0.02651	6.067	1.400	40.7756	
0.02349	3.267	1.400	40.7150	
0.02616	4.667	1.400	39.7830	
0.02609	1.400	1.400	39.5797	
0.02515	4.200	1.400	36.9344	
0.02503	2.333	1.400	36.5945	
0.02415	7.000	1.400	34.2486	
0.02417	2.800	1.400	34.1856	
0.02361	3.733	1.400	32.6049	
0.02340	5.133	1.400	32.0084	
0.02335	6.533	1.400	31.8684	
0.02333	5.600	1.400	31.8178	
0.02330	No change		31.7243	
<0.02330	Infeasible			

Initial distribution: $v(0) = 0$, $v(i) = 0.066667$, $i \neq 0$

<i>Bounds on discounted fraction of years $x_t \leq 0.933$</i>				
0.15580	Base stock at	0.933	656.721	1.2314
0.15580	1.867	1.400	656.721	1.2314
0.15299	3.267	1.400	611.634	1.1468
0.15212	6.067	1.400	597.667	1.1206
0.15206	4.667	1.400	596.745	1.1189
0.15187	1.400	1.400	593.696	1.1132
0.15041	4.200	1.400	554.016	1.0388
0.14909	2.333	1.400	548.917	1.0292
0.14690	2.800	1.400	513.729	0.9632
0.14543	3.733	1.400	490.039	0.9188
0.14487	5.133	1.400	481.101	0.9021
0.14474	7.000	1.400	479.004	0.8981
0.14468	5.600	1.400	478.026	0.8963
0.14466	6.533	1.400	476.623	0.8937
0.14455	No change		475.864	
<0.14455	Infeasible			

Initial distribution $v(i) = 1$ for all states i

TABLE 1 (Concluded)

Total fraction of years, ω	Change in policy		Value	$\frac{(1-\alpha)}{\sum_i v(i)}$ (value)
	State	Action		
<i>Bounds on discounted fraction of years $z_t \leq 0.467$</i>				
0.30498	Base stock at	0.933	43.78143	1.3134
0.25000	1.400	Randomized between 0.467, 0.933	42.98377	1.2900
0.16647	1.400 3.267	0.467 Randomized: 1.400, 0.933	41.7717	1.2532
0.16549	3.267 6.067	1.400 Randomized: 1.400, 0.933	41.0265	41.2308
0.16542	6.067 4.667	1.400 Randomized: 1.400, 0.933	40.9748	1.2292
0.16521	4.667 2.333	1.400 Randomized: 1.400, 0.933	40.8160	1.2245
0.16251	4.667 4.200	1.400 Randomized: 1.400, 0.933	38.7655	1.1630
0.16216	4.200 2.800	1.400 Randomized: 1.400, 0.933	38.4950	1.1549
0.16043	2.800 7.000	1.400 Randomized: 1.400, 0.933	37.1798	1.1154
0.16036	7.000 3.733	1.400 Randomized: 1.400, 0.933	37.1263	1.1138
0.15974	3.733 5.133	1.400 Randomized: 1.400, 0.933	36.6561	1.0997
0.15960	5.133 6.533	1.400 Randomized: 1.400, 0.933	36.5452	1.0964
0.15954	6.533 5.600	1.400 Randomized: 1.400, 0.933	36.5010	1.0950
0.15944	5.600	1.400	36.42505	1.0928
<0.15944	Infeasible			
Initial distribution: $v(0) = 0$, $v(i) = 0.066667$				

intermediate policies could be implemented, the shift between the two base stock sizes does not occur in any monotone fashion, that is, first all the larger (or smaller) stock sizes switch their policy, and then the other subset of states are switched over. This feature would make an intermediate policy easier to implement, but does not occur.

The fourth column in Table 1 $(1-\alpha)/\sum_i v(i)$ (value) is in a sense the "discounted mean" value of the harvest.

If $\bar{u}_x^y$ is the discounted fraction of years that state x is observed and action y is taken, and if G_x^y is the one-period return, then the fourth column is equivalent to

$$\sum_{x \in X} \sum_{y \in Y(x)} \bar{u}_x^y G_x^y$$

which is the one-period returns averaged over the discounted fraction of years it occurs. Hence, it is a "discounted mean" harvest (or value). Columns 1 and 4 of Table 1 provide the information needed by the

decisionmaker to determine the best trade-off between risk and return.

For the harvest-based probability constraints, an optimal policy is randomized for all alternative policies except for the original base stock policy of 0.933 and the final policy. The final policy is of some interest. Summarized it is

States	Harvest to	Harvest amount
0	0	0
0.467	0.467	0
0.933	0.933	0
1.400	0.467	0.933
1.867	0.933	0.933
>1.867	1.400	$x - 1.400$

This policy is very similar to an optimal policy that arises when "smoothing costs" (costs on the amount of year to year fluctuations in the allowed harvest) are added to the problem, with a positive cost only for decreasing the harvest (Mendelsohn 1978b). This suggests that smoothing costs act like a probabilistic constraint, most likely constraining the variance (or discounted variance) of the fraction of periods a state-action combination occurs.

Also, since randomized policies do not seem to occur in population-based constraints but do occur in harvest-based constraints, this leads to the following conjecture: If for every state that has at least one action included in a probabilistic constraint, all actions are also included in the probabilistic constraint, then a nonrandomized policy will be optimal. Otherwise, a randomized policy will be optimal whenever the probabilistic constraint is binding, except perhaps at the two extreme points.

A proof of the conjecture has not been found. But trying to find such rules are important. They lend the analyst insight into how to set up a problem both to obtain the desired trade-offs and to obtain policies that can be implemented. And ultimately, the purpose of all model building is the added insight they give to people who make the final decisions.

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Appendix

A lemma is needed before the theorems can be proven. Lemma 1 is a specialized version of theorem 3 in O'Brien (1975). The proof can be found in O'Brien (1975).

Lemma 1. Let $\{x_n, n \in N_0\}$ and $\{y_n, n \in N_0\}$ be two real-valued, discrete time Markov processes. If

ST.

(i) $x_0 \leq y_0$

(ii) $Pr\{x_{n+1} \geq t | x_n = x\} \leq Pr\{y_{n+1} \geq t | y_n = y\}$

for all t, n , and $x \leq y$

then there exists two new processes $\{\bar{x}_n\}$ and $\{\bar{y}_n\}$ such that on a common probability space Ω

- (a) $\bar{x}_n$ is distributed as x_n for all n
- (b) $\bar{y}_n$ is distributed as y_n for all n
- (c) $\bar{x}_n(\omega) \leq \bar{y}_n(\omega)$, for all n , and all $\omega \in \Omega$.

□

Proof of theorem 3.1: For any x_1 , the policy

$$y_1 = \min\{y_{\max}, x_1\}$$

can be shown to be stochastically dominant as follows. Let δ^* be this decision rule, and δ any other one-period decision rule. Then

$$Pr\{x_2 \leq \omega | x_1, \delta\} = Pr\{Ds[\delta(x_1)] \leq \omega\} = Pr\left\{D \leq \frac{\omega}{s[\delta(x_1)]}\right\}.$$

Since on the set $\{y : 0 \leq y \leq x_1\}$, $s[\delta^*(x_1)] \geq s[\delta(x_1)]$, then

$$\frac{\omega}{s[\delta^*(x_1)]} \leq \frac{\omega}{s[\delta(x_1)]}$$

or that δ^* is stochastically dominant over δ . This implies part (i) of lemma 1.

Conditioned on x_t , the policy

$$y_t = \min\{y_{\max}, x_t\} = \delta^*$$

compared with any other one-period decision rule δ can be shown to satisfy

$$Pr\{x_{t+1} \geq \omega | x_t, \delta^*\} \geq Pr\{x_{t+1} \geq \omega | x_t, \delta\}.$$

by the same argument as above. This is part (ii) of lemma 1, and hence the theorem is proven. □

Proof of theorem 3.2. Part (i): By assumption, π^* is stochastically dominant for x_2 given any x_1 . This is condition (i) of lemma 1.

Suppose for some $x_t^1 \leq x_t^2$, $x_t^1, x_t^2 \in X$, there exists a decision rule δ part of policy π , such that

$$Pr\{s[\delta(x_t^1), D_t] \geq \omega\} > Pr\{s[\delta^*(x_t^2), D_t] \geq \omega\} \quad \text{for some } \omega \in \Omega.$$

Since the D_t 's are i.i.d. random variables, this would imply

$$Pr\{s[\delta(x_1^1), D_1] \geq \omega\} > Pr\{s[\delta^*(x_1^2), D_1] \geq \omega\} \quad \text{for some } \omega \in \Omega.$$

However, this contradicts the assumption of the theorem that δ^* is a stochastically dominant decision rule for x_2 given x_1 . This contradiction implies condition (ii) of lemma 1.

Part (ii): The proof is by contradiction. Suppose a stochastically dominant policy exists, say $\pi^* = \{\delta_1^*, \delta_2^*, \dots\}$, but no one-period decision rule δ^* exists that is stochastically dominant. By assumption, any state except perhaps the absorbing state is reached with positive probability. Then, conditioned on x_t , there is no policy that is stochastically dominant for x_{t+1} , since by assumption δ^* does not exist, and the transition probabilities are stationary. This contradicts condition (ii) of lemma 1; from the proof of theorem 3 in O'Brien (1975) it is evident that this is sufficient to disprove that the chain resulting from π^* is stochastically dominant.

GROWTH OF NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, LARVAE IN THE SEA

RICHARD D. METHOT, JR. AND DAVID KRAMER¹

ABSTRACT

Northern anchovy larvae from 12 samples collected at 13.0°-16.2° C in the Southern California Bight were aged using daily growth increments in sagittal otoliths, and growth rates were calculated from size at age data. In nine samples, growth rate at 8 mm was very similar, ranging from 0.34 to 0.40 mm per day. Growth in the other three samples ranged from 0.47 to 0.55 mm per day. There was no correlation between growth rate and temperature within this set of field samples, but the range of growth rates was similar to the range expected from laboratory rearing experiments in this temperature domain. In no case was growth in the sea as slow as growth in the laboratory on severely limited rations. Anchovy larvae which obtain enough food to survive apparently obtain enough food to grow rapidly.

The presence of daily growth increments in some hard tissues of various plants and animals has been known for several decades (Neville 1967). Despite the fact that fish otoliths have been examined for annual growth marks throughout this century (Blacker 1974), daily growth increments were only recently identified in fish (Pannella 1971). The daily nature of these increments was verified in the laboratory by Brothers et al. (1976) using marine fish larvae. Taubert and Coble (1977) showed that increment formation in centrarchids is linked to the diel light cycle, not a feeding rhythm. Although studies have been conducted on the gross growth of otoliths (Degens et al. 1969; Mugiyu 1974, 1977) the physiological mechanism responsible for daily growth increment formation in fish is unknown (Simkiss 1974). Regardless, daily growth increments provide the ecologist with a tool for determining age and growth of specimens from the field (Struhsaker and Uchiyama 1976).

The objective of this project was to estimate growth of larval northern anchovy, *Engraulis mordax*, in the sea. Many laboratory studies demonstrate that growth of young fish is limited by temperature and ration (Riley 1966; Brett et al. 1969; O'Connell and Raymond 1970; Houde 1975). Because food availability is frequently considered to be one of the major factors controlling larval survival (Cushing and Harris 1973; Jones 1973;

May 1974; Lasker 1975; Arthur 1976), growth in the sea may frequently be limited by food. However, when collections of measured larvae are used for indices of spawner abundance or larval mortality studies, growth is assumed to be constant (Houde 1977) or a function solely of temperature (Bannister et al. 1974). Determining growth rates of larval fish in the sea should resolve this contradiction between theoretical and applied fishery science.

Anchovy larvae can be reared to metamorphosis and beyond in the laboratory (Kramer and Zweifel 1970; Hunter 1976; Sakagawa and Kimura 1976). Growth in these experiments was described best by the Gompertz growth equation, equation 1 (Kramer and Zweifel 1970; Zweifel and Lasker 1976). The effect of temperature on embryonic development and larval growth was incorporated by making the Gompertz growth parameters, A_0 and α , increasing functions of temperature (Zweifel and Lasker 1976; Zweifel and Hunter²). We compared the size at age of anchovy larvae in each field sample with that predicted by this temperature dependent model of anchovy growth in the laboratory, assuming that the temperature measured at the time of collection represented the temperature experienced by the larvae throughout their lifetimes.

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²Zweifel, J. R., and J. R. Hunter. Temperature specific equations for growth and development of anchovy, *Engraulis mordax*, during embryonic and larval states. (Manuscr. in prep.) Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038.

METHODS

Ichthyoplankton samples were collected from the Southern California Bight in March 1976, May 1976, and March 1977 with the NOAA ship *David Starr Jordan*. The sampling gear consisted of a CalCOFI (California Cooperative Oceanic Fisheries Investigations) ring net (1 m mouth diameter), MARMAP (Marine Resources, Monitoring, Assessment, and Prediction Program) Bongo net (60 cm mouth diameters), and a Manta neuston net; all with 505 μ m mesh. Oblique tows were made from the depth indicated in Table 1 to the surface. Samples were drained of excess seawater and preserved in 85% ethanol. (Recently we found that preservation is greatly improved if the alcohol is changed at least once after initial preservation; the otoliths may dissolve in poorly preserved samples with large plankton volumes. We change it once within 24 h and again within a few weeks.) Surface temperatures were measured with a bucket thermometer, and vertical temperature profiles were obtained with expendable bathythermographs.

The 12 samples analyzed in this study are from a limited part of the spawning range of the northern anchovy, but the Southern California Bight in March is an important spawning area for the central population of the anchovy (Smith 1972). Samples A1-A3 and B1 were collected near Los Angeles and the Channel Islands in 1976 (Figure 1) and were selected because of the wide size range of anchovy larvae found in each. Samples C1 and C2 were collected in this same region in March 1977. They were selected to represent the widest temperature range possible. Samples D1-D6 were collected in March 1977 along a transect extending seaward from San Diego and were the only samples containing anchovy larvae on this transect. Additional station data are in Table 1.

All fish eggs and larvae were sorted from the plankton samples chosen for analysis and anchovy larvae were processed in a manner similar to that described by Brothers et al. (1976). The standard length, tip of snout to tip of notochord or hypural plates, of each larva was measured to the nearest 0.1 mm. Sagittae were removed and placed on a microscope slide with the lateral (flat) side up. A polarizing filter and analyzer in the dissecting microscope made the otoliths more visible during dissection. The slide was air-dried and the otoliths were mounted under a coverglass with a clear mounting medium (Pro-texx³). Daily growth increments were counted in otolith images on a video screen; the total magnification by the microscope and video camera was 600 $\times$ or 1,500 $\times$. Each otolith was counted by 1-3 observers until the range of accepted counts for the two otoliths was ≤ 2 . Accepted counts were averaged over all observers and both otoliths.

The shrinkage of sea-caught larvae in preservative (Blaxter 1971) and the lag between hatching and first increment formation must be considered before comparing the size at age of sea-caught larvae with laboratory-reared larvae. Shrinkage of anchovy larvae depends upon the elapsed time between death and preservation (Theilacker⁴). There is no shrinkage when live larvae are placed directly into ethanol but a 5-15 mm larva could shrink about 0.6 mm if dead throughout the 6 min duration of the net tow. No shrinkage correction was applied because the elapsed time between death and preservation probably was <6 min and highly variable. Anchovy larvae tend to stay above the thermocline (Ahlstrom 1959) so are cap-

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

⁴Theilacker, G. H. Preservative shrinkage of larval anchovy, *Engraulis mordax*: laboratory versus field. Paper presented Nov. 1, 1978 at CalCOFI Conference, USC, Idyllwild, Calif.

TABLE 1.—Data on samples of larval northern anchovy taken from the Southern California Bight, spring 1976 and 1977.

Sample	Date	Time	Lat. N	Long. W	Gear	Depth (m)	Temperature (°C)	N
A1	29 Mar. 1976	2150	33°35.9'	117°56.6'	Ring	10	15.8	106
A2	31 Mar.	2205	33°43.5'	118°28.0'	Ring	5	15.0	38
A3	1 Apr.	1850	33°42.0'	118°20.5'	Ring	5	15.0	29
B1	8 May	1835	33°27.5'	118°40.0'	Manta	0	16.2	146
C1	20 Mar. 1977	1915	33°30.3'	118°01.5'	Bongo	70	15.1	35
C2	24 Mar.	2320	33°29.4'	117°54.1'	Bongo	70	13.0	112
D6	27 Mar.	0235	32°41.5'	119°01.5'	Ring	70	13.2	18
D1	27 Mar.	1830	32°00.0'	119°12.0'	Ring	70	14.0	13
D2	27 Mar.	2100	32°05.8'	118°55.0'	Ring	70	14.0	25
D3	28 Mar.	0140	32°28.8'	118°35.0'	Ring	70	14.4	18
D4	28 Mar.	0405	32°39.5'	117°59.5'	Ring	70	15.2	22
D5	28 Mar.	0630	32°47.0'	117°38.5'	Ring	70	15.1	25

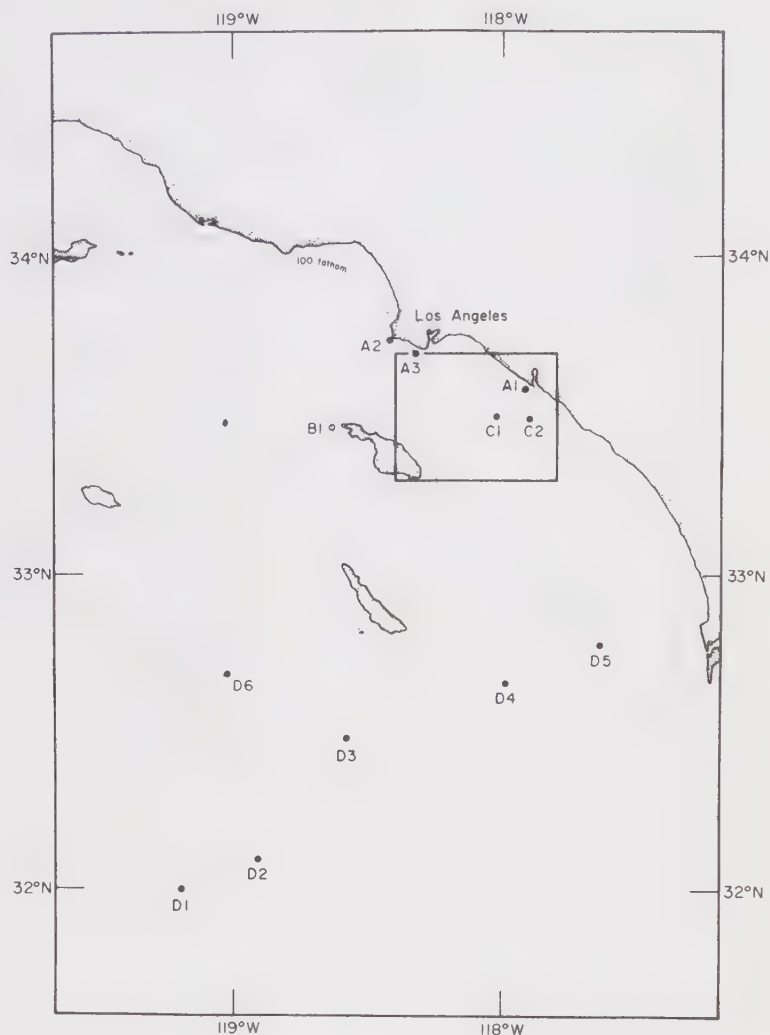


FIGURE 1.—Sampling sites for northern anchovy larvae off southern California. Box indicates the region shown in detail in Figure 4.

tured primarily during the last 1 or 2 min of an oblique tow, and some large larvae were still alive at the time of preservation.

Brothers et al. (1976) found a 5-day difference between posthatch age and number of increments for anchovy larvae reared in the laboratory at 16° C. At 19° C the lag is 3 days and at 12.5° C it is about 9 days (Methot unpubl. data). These lags are very close to the age at completion of yolk absorption (19° C, 2.9 days; 16° C, 4.7 days; 12.5° C, 8 days—Zweifel and Hunter (see footnote 2)); the larvae are about 4.2 mm at this age. Since developmental events, such as a functional jaw, occur at a constant size at all temperatures in this range (Zweifel and Lasker 1976), we assume that

increment formation also begins at a constant size of 4.2 mm at all temperatures. The number of increments represents the age in days after yolk absorption.

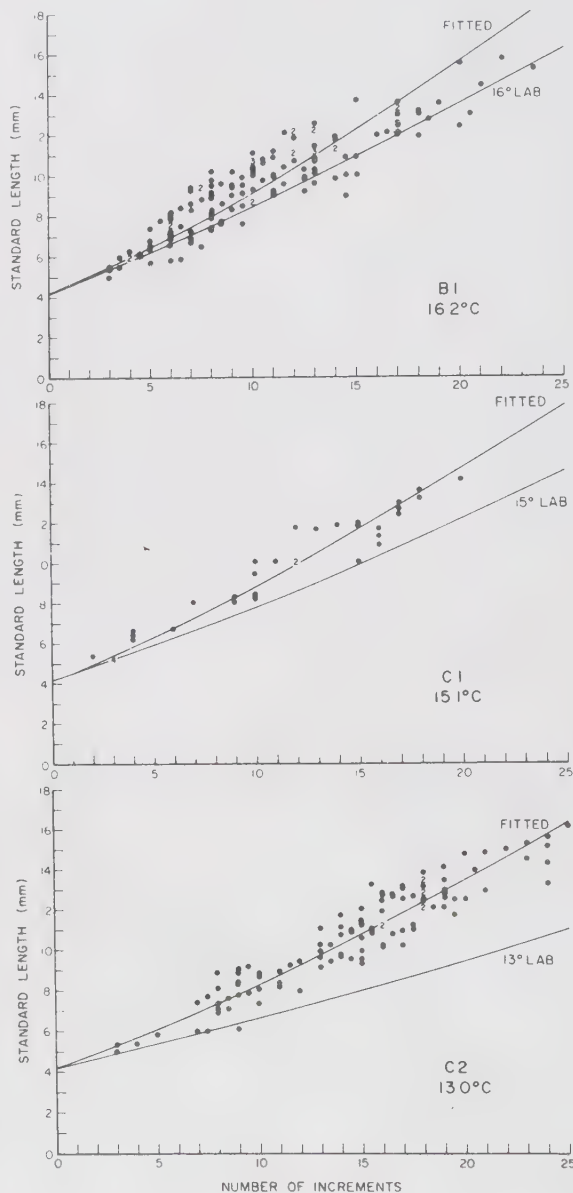
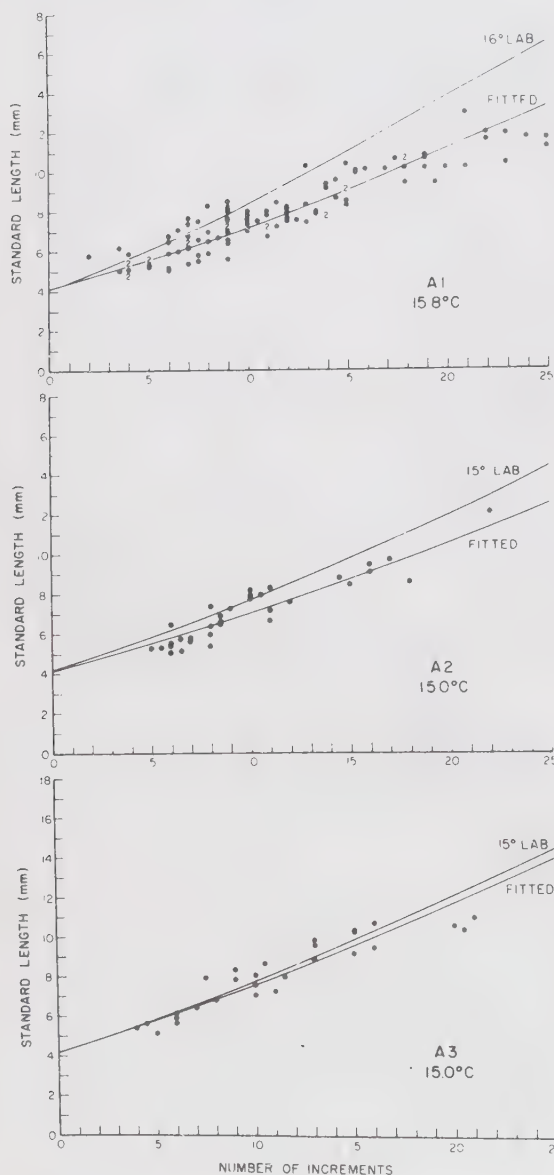
RESULTS

Standard length of each larvae in a sample was plotted against the mean number of increments (Figure 2). Each data point represents the integral of the growth rate of an individual larva over its lifetime, and a trend line through these points estimates the average growth history of larvae in the region sampled. Possible biases in this estimate of growth rate are discussed below.

According to the null hypothesis, the laboratory growth curve corresponding to the temperature at which the sample was taken should provide the best fit to the data. A suitable parametric procedure for testing this goodness of fit was not available. The nonlinear least-squares method for fitting the Gompertz growth function to size at age data (Zweifel and Lasker 1976) does provide estimates of confidence intervals on the parameters, but the probability levels associated with these intervals are only approximate (Conway et al.

1970). We found these confidence intervals to be rather broad.

We tested the goodness of fit by using a modification of the median regression procedure of Tate and Clelland (1957), replacing their estimated regression line by the laboratory derived Gompertz growth curve specified by our null hypothesis. Only curves at 1°C intervals were considered. Each larva in a sample was classified into a 2×2 contingency table, according to whether it was to the left or right of the median age of larvae in the



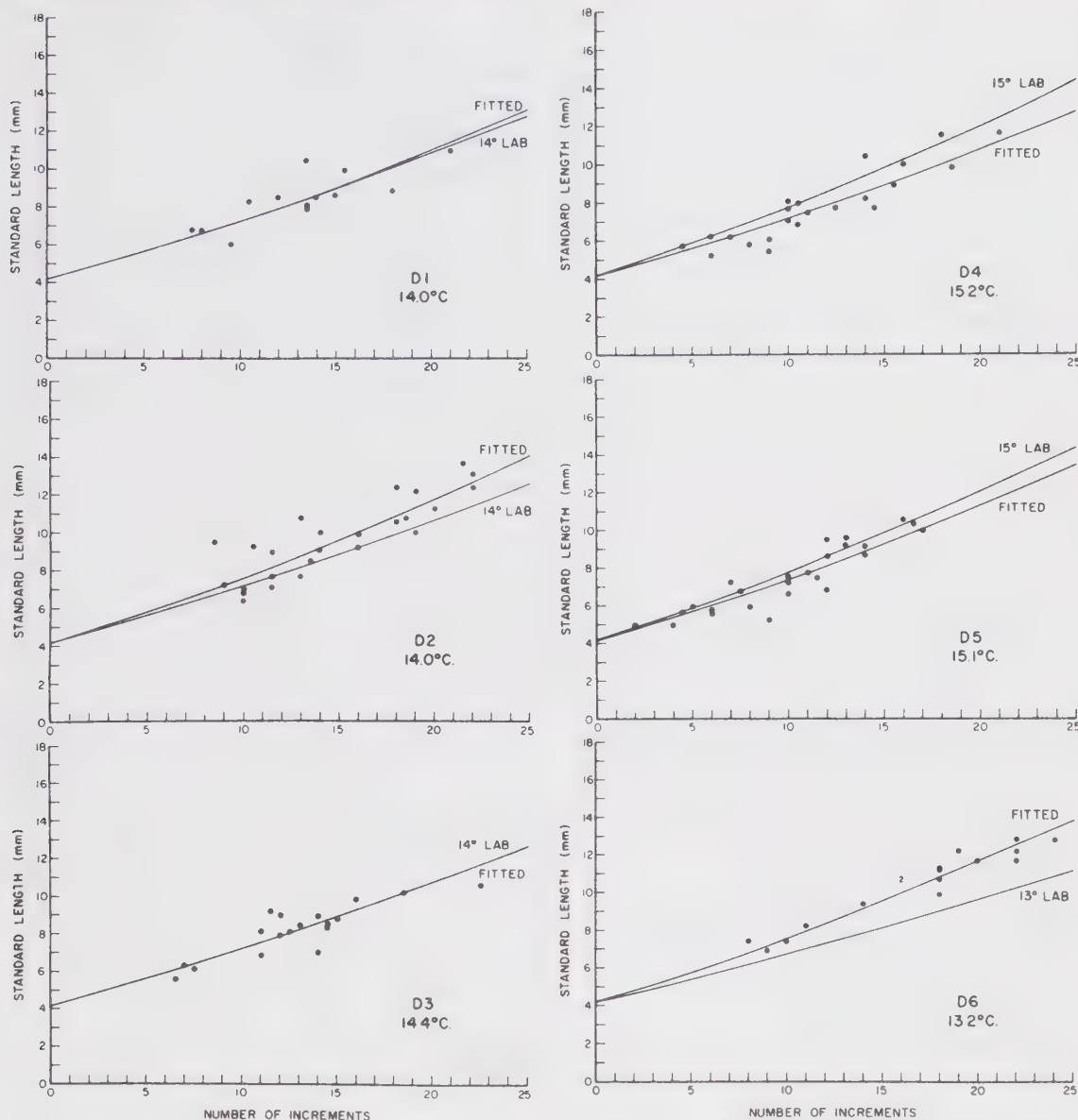


FIGURE 2.—Relationship between standard length of northern anchovy larvae and the number of daily growth increments (age postyolk absorption) in their otoliths. Two growth curves are shown. One (LAB) is the laboratory growth curve which was expected to fit the data because of the temperature at which the sample was collected. The other (FITTED) was fit to the data using a nonlinear least-squares method.

sample and whether it was above or below the laboratory growth curve (line labelled LAB in Figure 2). Points which fell on lines were split equally between the cells on either side of the line. A chi-square statistic with 2 degrees of freedom was calculated using the expectation of equal

numbers of larvae in each cell of the table. The results of these tests are in Table 2.

In general, larvae collected between Los Angeles and the Channel Islands in March 1976 (samples A1-A3) grew slower than expected while those collected there in March 1977 (C1, C2) grew

TABLE 2.—Results of chi-square test of the hypothesis (see text) that temperature-specific growth in the northern anchovy is the same in sea and laboratory (A-E) and the parameters of the Gompertz growth curve fit to the data in each sample (F-I). A, sample size; B, surface temperature in degrees Celsius; C, growth curve compared with data; D, probability that growth curve fits data; E, sign of significant deviations (0.05 level) from laboratory curve; F and G, Gompertz parameters, A_0 and α ; H, standard error of regression; I, growth rate at 8 mm (in millimeters/day). Last row shows results for combined data (samples with *).

Sample	A	B	C	D	E	F	G	H	I
A1*	106	15.8	16	<0.001	—	0.060	0.024	0.094	0.356
A2*	38	15.0	15	<0.01	—	0.059	0.025	0.089	0.341
A3*	29	15.0	15	<0.25	0	0.067	0.029	0.086	0.387
B1	146	16.2	16	<0.001	+	0.093	0.037	0.111	0.552
C1	35	15.1	15	<0.001	+	0.089	0.038	0.074	0.515
C2	112	13.0	13	<0.001	+	0.080	0.033	0.083	0.471
D6*	18	13.2	13	<0.001	+	0.067	0.029	0.059	0.389
D1*	13	14.0	14	>0.25	0	0.061	0.024	0.109	0.358
D2*	25	14.0	14	<0.025	+	0.068	0.029	0.120	0.397
D3*	18	14.4	14	>0.25	0	0.059	0.025	0.092	0.348
D4*	22	15.2	15	<0.10	0	0.061	0.027	0.105	0.348
D5*	25	15.1	15	>0.25	0	0.064	0.027	0.103	0.371
*						0.063	0.027	0.097	0.370

faster than expected. The larvae collected in March 1977 along the transect extending seaward from San Diego (D1-D6) grew about as fast as expected, given the surface temperature at which the sample was collected.

Since the data in 7 of 12 samples deviated significantly from the predicted Gompertz growth curve, we fit the Gompertz growth function (Zweifel and Lasker 1976)

$$\log_e (SL) = \log_e (SL_0) + \frac{A_0}{\alpha} (1 - e^{-\alpha t}) \quad (1)$$

where SL = standard length in millimeters
 t = number of increments = age in days postyolk absorption
 SL_0 = initial size, fixed at 4.2 mm
 A_0, α = parameters to be estimated

to each using a nonlinear least-squares method (Conway et al. 1970).

The parameters of the fitted curves (Table 2) were used to calculate a linear approximation of the growth rate of 7.5-8.5 mm anchovy larvae (Figure 3). The range of growth rates among the 12 samples collected at 13°-16.2° C was bounded by the growth rates of anchovy larvae grown in the laboratory at 14° and 17.5° C. Growth was very similar in all but three samples (B1, C1, C2) although the temperatures associated with these nine samples spanned a range of 2.5° C. The growth rate of 8 mm larvae calculated from a Gompertz curve fit to the combined data of the nine similar samples was 0.37 mm/day. The mean

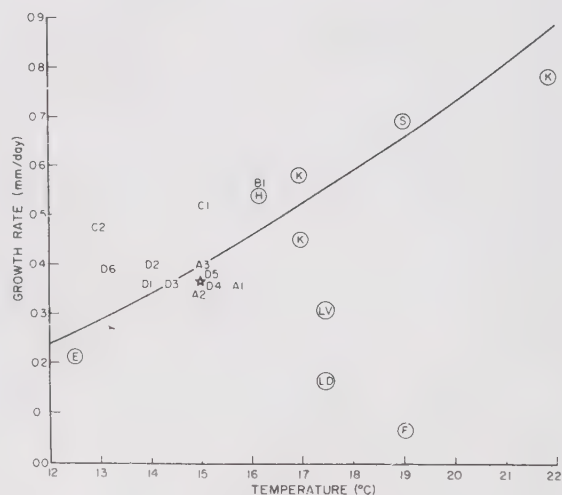


FIGURE 3.—Relationship between growth rate (millimeters/day at 8 mm) and temperature for northern anchovy larvae from the field (bare symbols) and in the laboratory (circled symbols). Field samples, this study, A1-D6; composite of nine field samples, B1, C1, and C2 not included, ☆; Hunter 1976, laboratory-reared prey, H; Kramer and Zweifel 1970, wild plankton for food, K; Lasker et al. 1970, dinoflagellates only, L, D, dinoflagellates plus veliger, LV; Sakagawa and Kimura 1976, S; unpubl. data available at Southwest Fisheries Center, low temperature experiment, E, periodic starvation experiment, F. Curve was derived from the model of Zweifel and Hunter (see text footnote 2); it was not fit to the growth rate data presented here.

temperature of these nine samples (weighted by number of larvae) was 15.04° C. The model of Zweifel and Hunter (see footnote 2) predicts that 8 mm larvae reared at 15° C would grow at 0.395 mm/day.

Standard deviation of $\log_e$ (size) at age, calculated from the set of combined data, ranged from 0.045 at 4 increments to 0.144 at 19 increments with a mean of 0.0904. The standard error of regression (standard deviation of residuals) of the Gompertz curves fit to the data (Table 2) were similar to these estimates of standard deviation of size at age. Any difference in growth rate between these samples, small scale environmental heterogeneity integrated by our nets, or random error in the aging of the larvae causes the standard error of regression to overestimate variability in the growth process. Over the same age range in a laboratory experiment (Hunter 1976), standard deviation ranged from 0.064 to 0.153 with a mean of 0.115.

EVALUATION OF POTENTIAL BIASES

The conditions under which larvae are reared and growth is measured in the laboratory may differ sufficiently from conditions in the sea to bias the comparison of growth in the sea with growth in the laboratory. In the laboratory, growth is estimated from a time series of samples from a cohort. The exact age of each larva is known; temperature rarely varies $>1^\circ\text{C}$; prey concentration is rather constant; and mortality is low (about 3%/day in Hunter 1976) and except for cannibalistic species, not influenced by size-selective predation. Growth of sea-caught larvae is estimated from one sample containing larvae of several ages. The age of each is estimated from the number of daily growth increments in its otoliths, the environmental conditions are measured only when the sample is taken, mortality is over 10%/day (Smith and Lasker 1978) and probably size selective, and large larvae avoid the net disproportionately.

Age Determination

Anchovy larvae deprived of food at the normal time of first feeding may delay deposition of daily growth increments until food is provided and growth resumes (Theilacker⁵), but if larvae are still about 4.2 mm when the first increment appears, estimates of the growth rate of larger larvae will be unaffected. Taubert and Coble (1977) found that increment formation in late larval and juvenile centrarchids stopped if growth was

slowed sufficiently by low temperature. We examined the otoliths of some anchovy larvae whose growth was drastically retarded by a reduction in rations (Methot unpubl. data) (F in Figure 3). The slowest growing of these larvae had fewer increments than expected, so increment formation can stop before the point of no return is reached. However, if we use number of increments rather than known age to estimate growth rate of these laboratory-reared larvae, the resulting overestimated growth rate is still slower than that observed in any field samples used in this study. We conclude that the sea-caught larvae were growing fast enough to deposit a growth increment every day.

Temperature Determination

Anchovy larvae usually remain above the thermocline (Ahlstrom 1959), so surface temperature probably accurately represents the temperature they experience. Growth was slower than expected in March 1976, but it is unlikely that the surface temperature overestimated the temperature experienced by the larvae because these samples were all collected shallower than 10 m (Table 1). Positive deviations in growth rate, equivalent to a temperature change of up to 3°C , were observed in March 1977, but additional temperature data collected at that time indicate that the measured surface temperature accurately represented the temperature experienced by the larvae throughout their lifetimes. The relative surface temperature field determined from satellite observations of infrared radiation (Bernstein et al. 1977), taken just before and after this 2-wk cruise, was entirely consistent with the temperature field measured during the cruise; there was no cooling trend. The resolution of the satellite observations was insufficient to distinguish details of the eddy structure in the region of samples C1 and C2, but here the greater intensity of surface temperature determinations allowed contouring of isotherms for the first 4 days of the cruise and the next 5 days (Figure 4). Samples C1 and C2 were taken within persistent water masses of about 10 km width, not in regions with steep horizontal gradients in temperature. Because of the shallow thermocline in this region ($<5\text{ m}$ at some stations), we may have overestimated the temperature experienced by the larvae but this would cause a negative deviation from the model, not the observed positive deviations.

⁵G. H. Theilacker, Southwest Fisheries Center La Jolla Laboratory, NMFS, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1978.

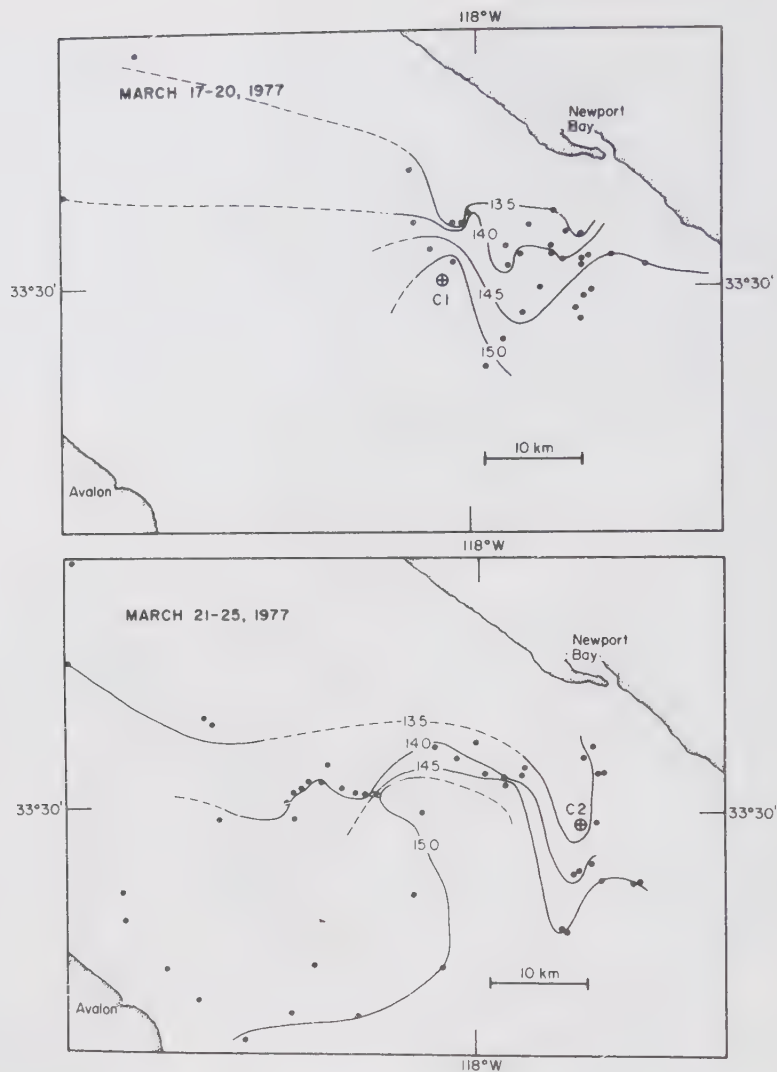


FIGURE 4.—Surface isotherms in degrees Celsius between Los Angeles and Santa Catalina Island, Calif., in March 1977.

Selective Mortality

If mortality rate is a function of size, then growth rates determined from size at age data will provide a biased estimate of the true growth rate of the survivors which are sampled (Ricker 1969). The effect of size selective mortality on our estimates of growth is difficult to assess. Few sets of data are extensive enough to even consider the question of ontogenetic changes in mortality rate of larval fish. All available estimates are based upon sized but not aged specimens. They depend upon an assumed growth curve (Farris 1960) and are susceptible to bias by size selective avoidance of the sampler. Smith (1973) found a difference in

mortality rate between sardine eggs and young sardine larvae, but mortality in plaice was essentially constant through the egg and larval stages (Bannister et al. 1974). Laboratory experiments show that older, more active yolk-sac anchovy larvae are less susceptible than newly hatched larvae to some invertebrate predators (Lillelund and Lasker 1971; Theilacker and Lasker 1974). As a rough estimate of the magnitude of the maximum effect of size selective mortality on our growth estimates, we examined the interaction between variable growth and size selective mortality and determined the effect of this mortality on mean size of anchovy larvae at 25 days after yolk absorption.

Suppose variation in growth is such that individuals of age 25 days range in size from 11.4 to 16.6 mm and that the exponential growth rate parameter which gives rise to this variation has a uniform statistical distribution. If mortality during this 25-day period is random with respect to size, the mean size of individuals which survive to age 25 days will be 13.86 mm. However, if the instantaneous daily mortality rate is related to size by $M = 3.5 L^{-2}$ (this is consistent with current estimates of egg, young larvae, and adult mortality rates for anchovy (MacCall 1974; Smith and Lasker 1978)), the mean size of individuals which survive to age 25 days will increase only slightly to 14.08 mm. We conclude that an overestimate of growth because of size selective mortality is unlikely to occur.

Another possibility is that mortality is related to growth rate rather than size, the mortal fraction being that portion of the population which is slow growing and weak and therefore more susceptible to predators (Isaacs 1964). If we make the extreme assumption that the daily mortal fraction is the slowest growing 10% of the cohort, the survivors at age 25 days will be the fastest growing 7% of the original cohort, but this extreme model unrealistically predicts that variations in size at age would decline as the slow growing larvae die. Some intermediate degree of growth rate selective mortality could affect estimates of growth rate in the sea, especially if mean growth rate is slow and the slower growing individuals are near starvation.

Net Avoidance

Avoidance of the ring net by anchovy larvae in daylight begins at a length of about 5 mm and increases with size (Lenarz 1973; Murphy and Clutter 1972). The Bongo net catches larvae more effectively but avoidance still occurs in the larger size classes. The degree to which we underestimated mean size at age depends upon how rapidly avoidance increases with increasing size. We attempted to minimize this bias by only considering larvae with fewer than 25 increments (lengths less than about 15 mm) and samples taken at twilight or dark. There was no difference in size at age between the twilight samples (D1, D5) and the night samples (D2-D4) along the transect. Although fast growth was observed only in samples taken with the Bongo or neuston net (B1, C1, C2), we do not believe this was an artifact caused by size-selective avoidance of the ring net. If this

were an artifact, then ranges in size at age in samples taken by the less selective gear would have been broader and overlapped the distribution of size at age in samples taken with gear which allowed larger larvae to escape. This was not observed.

DISCUSSION

Growth rates of larval northern anchovy <1 mo old were determined with size at age data. In 9 of 12 samples, growth rates at 8 mm were very similar, ranging from 0.34 to 0.40 mm/day. The growth rate estimated from the combined data of these samples was 0.37 mm/day. Growth in the three other samples was faster, 0.47-0.55 mm/day. Variation in size at age between individuals was small. A typical 95% confidence interval for larvae with 12 daily growth increments was 6.5-9.5 mm.

When the trend of growth rate on temperature, obtained from several rearing experiments, was compared with the field results (Figure 3) it was obvious that growth in the sea was similar to growth in the laboratory. The range in growth rate between field samples at the same temperature was similar to the range in growth rate between laboratory rearing experiments conducted at the same temperature (Kramer and Zweifel 1970). Variation of size at age was also similar in the sea and the laboratory. In no case were sea-caught larvae growing as slowly as larvae reared in the laboratory on inadequate rations (LV, LD, F in Figure 3). At 17.5° C (Lasker et al. 1970) anchovy larvae fed only a dinoflagellate grew at about 0.15 mm/day (LD) and larvae fed dinoflagellate and veligers (LV) grew still slower than larvae fed wild plankton (K) (Kramer and Zweifel 1970). Although the availability of suitable prey may limit the feeding success rate of first feeding anchovy larvae (Lasker 1975), larvae which get enough food to survive apparently get enough food to grow rapidly.

There was no obvious relationship between growth rate and temperature. This is not surprising considering the narrow temperature range considered, the variation in growth rate between laboratory experiments at the same temperature, and the uncertainty in our measurement of the temperature experienced by the larvae in the sea. The samples we examined came from near the center of distribution of northern anchovy larvae with respect to space, time, and temperature. As samples from the periphery of this species range

become available, we expect to find increased variation in growth rate.

Correlations between the spatial-temperature pattern of variation in growth rate and environmental parameters may provide clues to the events which control larval survival. This analysis will require that the measured growth rates reflect the larvae's response to the environmental factors measured at the time the sample was collected. We estimated the growth rate of larvae in a sample by determining the relationship between size (L) and age (T). This technique is susceptible to several biases discussed above and is not sensitive to changes in growth conditions occurring a few days before the sample is taken. If the instantaneous growth rate of each individual could be measured, then the same growth rate parameters could be estimated from the relationship between dL/dT and L . This alternative method would reflect growth conditions at the time of sampling and would be independent of changes in growth conditions during the lifetime of the older larvae in the sample. Ottaway and Simkiss (1977) developed a relative measure of the instantaneous growth rate of adult fish using the in vitro rate of incorporation of ^{14}C labelled glycine into scales, but this technique may not be adaptable to larval fish. Another approach is to correlate the width of a daily growth increment with the growth of the fish on that day. A measurement of the width of the outer increments could provide an absolute measure of growth rate during the few days before capture.

In addition, the radius of each increment in an individual's otoliths could be used to back calculate its growth history (Ricker 1969). The difference between the back calculated growth histories of older individuals, the survivors captured with nonselective gear, and the distribution of size at age of all younger individuals supplies information on differential mortality and size dependent net avoidance by the larvae. Ultimately, analysis of daily growth increments in the otoliths of larval fish may provide a means of determining whether larval survival is limited primarily by predation or food and how these two factors interact.

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COASTAL UPWELLING OFF WESTERN NORTH AMERICA, 1976

Craig S. Nelson

INTRODUCTION

The nearshore marine environment off western North America is markedly influenced by processes of coastal upwelling and downwelling. Upwelling is widely recognized as a fundamental factor in the formation of nutrient rich surface water favorable to primary production. Wind induced surface layer divergence may also dramatically modify nearshore marine climate, and may act as an important driving mechanism for continental shelf/slope circulation.²

Variations in biological communities often occur nearly in phase with the predominant seasonal cycle of coastal upwelling. Major fluctuations in the intensity of coastal upwelling also occur at frequencies corresponding to the diurnal sea breeze, to synoptic "events", and to interyear variations in the location and intensity of the large scale atmospheric circulation system over the northeastern Pacific. Anomalously strong or weak upwelling may be related to major fluctuations in stock recruitment (Parrish 1976) which are likely to have subsequent effects higher in the food chain.

Bakun (1973) computed an index of coastal upwelling based on calculations of surface wind stress derived from analyzed fields of surface atmospheric pressure. These fields are routinely produced by the U.S. Navy Fleet Numerical Weather Central. The "upwelling index" is defined as the offshore directed component of Ekman transport, and is considered to be a gross measure of the amount of upwelling required to replace water transported offshore in the surface layer. Negative values of this index

¹Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93940.

²Nilner, P. P., and C. N. K. Mooers. 1977. A model shelf dynamics program. A report to the National Science Foundation, Office of the International Decade of Ocean Exploration, January 1977.

indicate onshore surface transport and downwelling at the coast. Monthly mean upwelling index values for the period 1946-71 were presented for the 15 locations shown in Figure 6.1. These time series have been updated for 1972-74 and 1975 (Bakun 1976, 1978).

Monthly upwelling indices for 1976 are given in Table 6.1. Anomalies from the 20-yr (1946-67) mean monthly values are presented in Table 6.2. Upwelling indices are displayed in percentiles in Figure 6.2. Percentile values were based on the rank of the upwelling index for each month and location within the 31-yr (1946-76) time series.

THE GULF OF ALASKA

wind driven surface transport in the Gulf of Alaska (60N, 149W to 51N, 171W) tends to be divergent in the interior and convergent at the coast.³ The annual cycle of coastal convergence is dominated by vigorous downwelling during the winter season, when intense cyclonic storm activity characterizes the atmospheric circulation in the region. During 1976 monthly upwelling indices were negative along both northern and eastern boundaries, except in June and July when small positive values were evident.

In January more intense than normal downwelling was indicated along the eastern boundary, while positive anomalies occurred in the northern Gulf of Alaska. This pattern of anomalies reversed the trends for these two areas begun during the last quarter of 1975 (Bakun 1978). The remainder of the first quarter of 1976 was marked by less intense than normal winter downwelling. Reduced levels of coastal convergence may be associated with less intense than normal surface divergence offshore. A decrease in the strength of the coupled "pumping" between the central Gulf of Alaska and the coast would tend to reduce the baroclinicity established during the previous three months.

More intense than normal coastal convergence was evident during the remaining months of 1976. A general pattern of upwelling indices below the median (Fig. 6.2) was interrupted in June, when small positive values occurred, and in October, when an irregular transition to vigorous winter downwelling was apparent. Anomalies from the long-term monthly means (Table 6.2) were negative from April through September, except during June, at

³ Ingraham, W. J., Jr., A. Bakun, and F. Favorite. 1976. Physical Oceanography of the Gulf of Alaska. U.S. Dep. Commer., NOAA, NMFS, Northwest Fish. Cen., Processed Rep., 132 p.

these five locations. Upwelling indices at 54N, 134W and 51N, 131W for May and July were the lowest (largest negative values) calculated in the 31-yr time series. Coastal convergence continued through the summer at approximately one-half the intensity of the preceding winter's downwelling. Under these conditions, the existing baroclinic structure would tend to be maintained. This situation contrasts with more typical relaxed summer conditions, in which the baroclinicity established during a previous winter is dissipated.

A smooth transition to vigorous winter downwelling was replaced by less intense than normal downwelling in October. This period of positive anomalies immediately followed and preceded several months of large negative anomalies. An examination of the monthly mean surface atmospheric pressure field for October (not shown) indicated a westward shift, relative to the long-term mean position, of the center of the low pressure system and a much reduced pressure gradient near the coast. A return to near normal (50th percentile) winter downwelling occurred in December.

VANCOUVER ISLAND TO POINT CONCEPTION

The stretch of coast from Vancouver Island (48N) to Point Conception (36N) is a transition zone, in which wind driven surface transport changes from predominantly onshore to predominantly offshore. During 1976 this entire coastal region was characterized by a pattern of three periods of more positive than normal upwelling indices separated by two short intervals of more negative than normal indices. These features repeat the general pattern noted in the previous section, and indicate a degree of coherence in the large scale atmospheric circulation on space scales approaching 1,200 km and on time scales of two to four months.

Neah Bay to Central Oregon (48N, 125W to 45N, 125W). Large positive anomalies in January extended a period of relaxed coastal convergence first noted in December 1975 (Bakun 1978). This trend did not continue; near normal downwelling was indicated from February through April along the coasts of Washington and northern Oregon. A prolonged period of relaxed coastal upwelling from May to September was interrupted in June by a return to near normal index values. However, this feature appeared as an anomaly in a pattern of upwelling indices below the median, in a region stretching from the northern Gulf of Alaska to Oregon. Upwelling peaked in June, somewhat earlier than the long-term mean values would indicate (Bakun 1973). Fall and early winter were characterized by a return to negative mean values (coastal convergence), although positive anomalies indicated less intense than normal downwelling.

Cape Blanco to Point Conception (42N, 125W to 36N, 122W). The patterns of positive anomalies during winter and negative anomalies during summer noted above were not repeated exactly along the coasts of southern Oregon and northern California. This stretch of coast encompasses the core of the California Current upwelling region, which is characterized, in the mean, by a maximum in the alongshore component of surface wind stress during July (Nelson in press). In 1976 the timing, duration, and intensity of the indicated upwelling at Cape Blanco (42N), Cape Mendocino (39N), and to a lesser extent Point Conception (36N), were markedly different than the 1946-67 long-term mean conditions.

Positive anomalies occurred in January and February, during a part of the year ordinarily characterized by coastal convergence. Although onshore transport was indicated at 42N, upwelling indices for 39N were positive and were clearly above the 50th percentile. This feature continued a long trend of positive anomalies which began in April 1975 (Bakun 1978).

The onset of anomalous upwelling appeared to occur rather abruptly in March. The timing of this event was coherent at three locations along the coast (Fig. 6.2). Near Cape Mendocino (39N), the March index was nearly a factor of three greater than the long-term mean value for this month and location. A return to near normal conditions occurred in April.

Conditions favorable to strong coastal upwelling reappeared in May, June, and July. Monthly mean indices exceeded the 80th percentile at both 42N and 39N. The values computed for Cape Mendocino (39N) were the second highest in May, and the third largest in June within the 31-yr series. This recurrence of unusually large positive anomalies marked the fourth consecutive year in which stronger than normal coastal divergence has been indicated. Such long-term persistence possibly suggests either a shift in, or intensification of, the large-scale atmospheric circulation influencing the west coast of North America. The timing of the summer upwelling season was also somewhat unusual. Index values peaked in May, two months earlier than the peaks in the long-term mean cycles for these locations.

A rapid transition to below normal upwelling (i.e., negative anomalies) during August was immediately followed by a return to large positive anomalies in September. The period of relaxed upwelling in August was notable, since negative anomalies during this month were evident along the entire stretch of coast from the northern Gulf of Alaska to the Southern California Bight.

The pattern of positive anomalies persisted through the last quarter of 1976. While the upwelling indices at 42N approached the 20-yr mean values (i.e., downwelling), indices exceeding the

80th percentile occurred in September and October at Cape Mendocino. The indices for November and December showed a gradual return to median values; however, upwelling was still indicated for 39N. As Bakun (1978) has already noted, such a prolonged period of upwelling would appear to be favorable for those fish stocks dependent upon upwelling based primary production.

POINT CONCEPTION TO BAJA CALIFORNIA

A secondary California Current upwelling regime along this coast (33N, 119W to 21N, 107W) is characterized by positive values of offshore transport throughout the year (Bakun and Nelson in press). Maximum upwelling index values occur from March to May and coincide, in time, with major peaks in spawning.

Although the upwelling index remained positive during 1976, the most prominent features were the extended periods of large negative anomalies in January and February, and again from August to December. This pattern marked an almost complete reversal of the conditions which prevailed in 1975. During the previous year, below median values occurred in summer, while above median indices were evident in spring and fall.

Positive monthly mean anomalies were evident from March to August (Table 6.2). Much more intense than normal upwelling at locations from Punta Eugenia (27N) to Cabo San Lucas (21N) extended the upwelling season to late summer. This period was immediately followed by a decline to large negative anomalies. This pattern of negative anomalies during fall and early winter encompassed the entire region from Point Conception (36N) to Cabo San Lazaro (24N). Upwelling indices were consistently below the 30th percentile, which suggested extremely relaxed upwelling for this time of year.

The pattern of negative anomalies corresponded in time and in location with a rapid warming of surface water during fall and winter. The intensity of warming was indicated by December sea surface temperature anomalies 2C warmer than the 1946-67 mean, and more than 3C warmer than the temperatures during the 1975 winter season.⁴ Relaxed upwelling (i.e., small values of offshore transport) is correlated with northward surface flow

⁴Fishing Information, No. 12, December 1976. Southeast Fisheries Center, NMFS, NOAA, La Jolla, CA 92038.

near the coast.⁵ The upwelling conditions during fall and winter 1976 indicated the possibility of a major intrusion of warm southern water which could have extended beyond Point Conception.

RELATION TO FISHERIES

Within the coastal region from Point Conception (33N) to Cabo San Lucas (21N), upwelling and upwelling related processes may be important transport mechanisms for fish stocks which spawn in the area.⁶ The five months of below normal indices in this region followed a period of moderate upwelling at 30N, 119W. On the basis of above normal upwelling at this location during peak spawning, recruitment models predicted better than average reproductive success for Pacific mackerel in 1976.⁷ Relaxed upwelling during the fall and increased northward flow near the coast would tend to favor northward transport of the southern stock of Pacific mackerel, Scomber japonicus, which would increase the estimates of the 1976 year class above those predicted on the basis of spring upwelling alone. Current market evidence indicates that, indeed, the 1976 year class is much stronger than had been anticipated.⁸

⁵Nelson, C. S. 1976. Seasonal variations in processes related to the California Current. Paper presented at the 23rd Eastern Pacific Oceanographic Conference, September 29-October 1, 1976.

⁶Parrish, R. H., and C. S. Nelson. Fish stocks and the California Current. Paper presented at the Calif. Coop. Oceanic Fish. Invest. Conference, November 16-18, 1976, Palm Springs, CA. Unpubl. manuscript.

⁷R. H. Parrish, Pacific Environmental Group, NMFS, NOAA, Monterey, CA 93940. Pers. commun.

⁸R. A. Klingbeil, California Fish and Game Comm., Long Beach, CA 90802. Pers. commun.

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Table 6.1 - Monthly coastal upwelling indices for 1976. Units are cubic meters per second per 100m length of coast. Negative values indicate onshore transport of surface waters and resultant downwelling.

	<u>JAN</u>	<u>FEB</u>	<u>MAR</u>	<u>APR</u>	<u>MAY</u>	<u>JUN</u>	<u>JUL</u>	<u>AUG</u>	<u>SEP</u>	<u>OCT</u>	<u>NOV</u>	<u>DEC</u>
60N 149W	-85	-91	-10	-16	-2	4	2	-1	-17	-12	-68	-94
60N 146W	-113	-104	-13	-26	-4	8	2	-2	-33	-22	-123	-146
57N 137W	-201	-50	-35	-54	-35	6	-6	-8	-81	-58	-237	-132
54N 134W	-159	-18	-40	-55	-55	5	-26	-7	-56	-39	-163	-86
51N 131W	-81	1	-16	-33	-21	20	-23	4	-12	-6	-68	-48
48N 125W	-63	-35	-24	-3	6	31	5	9	1	-6	-37	-53
45N 125W	-41	-30	-10	-0	21	56	23	17	14	-0	-31	-47
42N 125W	-10	-4	20	15	132	166	95	44	52	7	-23	-27
39N 125W	9	9	101	59	331	304	249	111	134	79	2	3
36N 122W	22	20	124	115	259	196	224	109	80	49	4	1
33N 119W	-1	34	120	198	304	262	277	212	88	50	4	-6
30N 119W	44	64	139	160	231	199	160	145	70	80	54	28
27N 116W	27	51	127	158	215	214	142	170	57	58	28	17
24N 113W	24	50	127	153	191	172	107	86	57	72	34	32
21N 107W	21	33	122	125	119	36	30	4	1	16	18	35

Table 6.2 - Monthly coastal upwelling index anomalies for 1976 relative to the 20-year (1948-67) mean value for each month and location. Units are cubic meters per second per 100 m length of coast.

	<u>JAN</u>	<u>FEB</u>	<u>MAR</u>	<u>APR</u>	<u>MAY</u>	<u>JUN</u>	<u>JUL</u>	<u>AUG</u>	<u>SEP</u>	<u>OCT</u>	<u>NOV</u>	<u>DEC</u>
60N 149W	54	-5	36	-5	-2	-2	-4	-6	-14	14	5	14
60N 146W	67	-2	35	-14	-2	1	-3	-5	-24	12	-29	-17
57N 137W	11	67	16	-30	-25	6	-8	-2	-52	29	-96	31
54N 134W	-63	49	-12	-35	-46	5	-29	-7	-33	43	-65	5
51N 131W	-17	37	-4	-27	-25	5	-39	-9	-9	34	-10	9
48N 125W	27	12	-3	-3	-11	5	-29	-13	-3	33	51	47
45N 125W	53	18	5	-9	-13	8	-51	-34	-3	20	42	46
42N 125W	57	24	16	-18	53	63	-36	-47	16	7	19	31
39N 125W	21	0	65	-10	207	136	68	-28	71	59	8	16
36N 122W	12	-15	44	-5	56	-43	25	-73	-14	0	-8	-6
33N 119W	-20	-14	-0	20	21	-50	46	-0	-49	-26	-18	-16
30N 119W	-12	-14	23	19	31	-0	17	3	-59	-23	-11	-26
27N 116W	-45	-43	8	10	13	19	28	65	-54	-48	-46	-46
24N 113W	-26	-24	34	36	49	44	59	42	8	3	-19	-8
21N 107W	3	-7	25	25	32	-3	27	-2	15	31	10	26

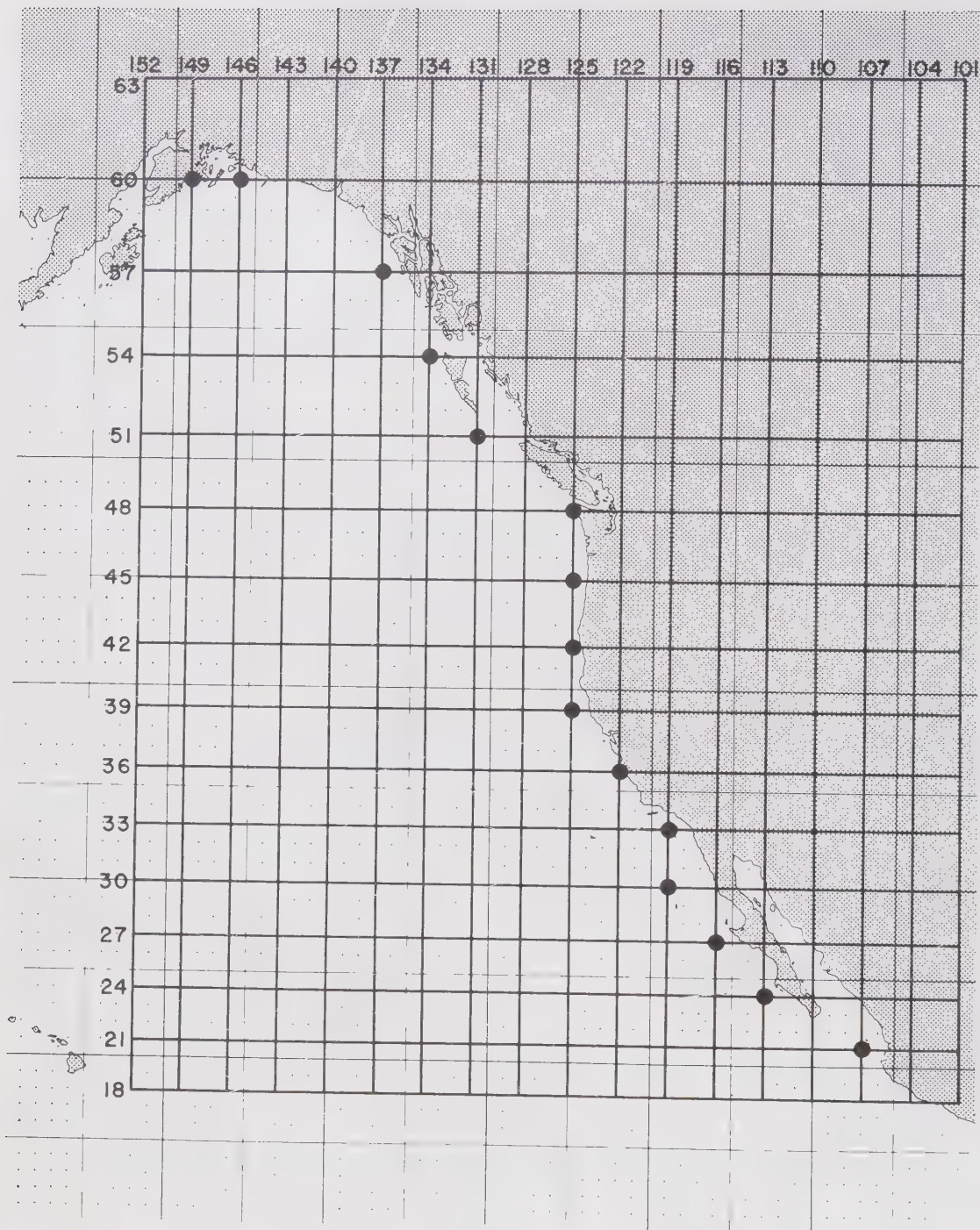


Figure 6.1.—Computation grid. Intersections at which upwelling indices are computed are marked with large dots.

PERCENTILIZED MONTHLY MEAN UPWELLING INDICES

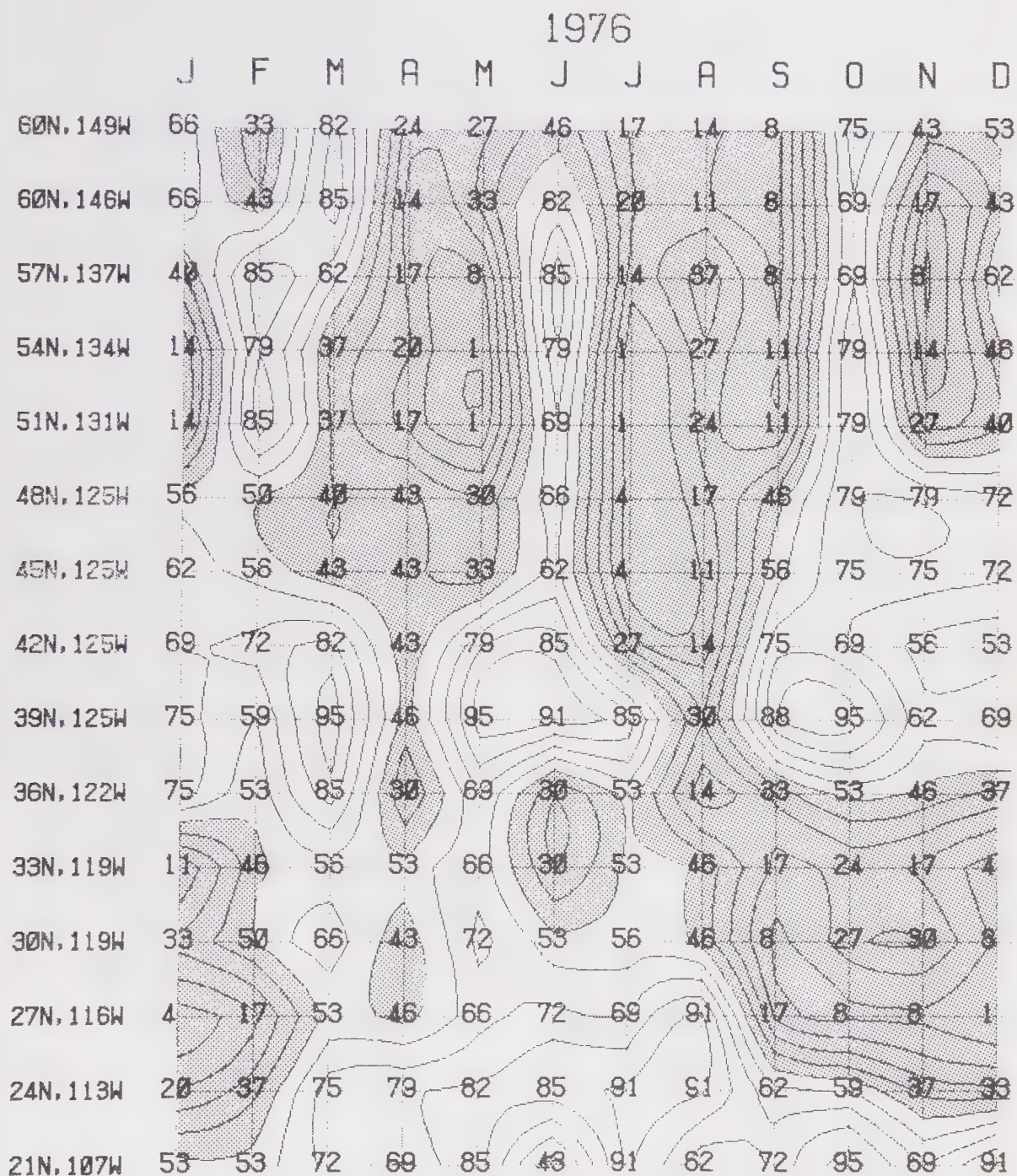


Figure 6.2.—Percentalized upwelling index values for 1976. Percentiles indicate relative ranking within the 31-yr data set for each month and location. The contour interval is 10 percentile units. Values below the median (50th percentile) are shaded.

DENSITY ESTIMATION BY VARIABLE AREA TRANSECT

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Abstract: The frequency distribution of the distance from a randomly selected point to the r th nearest organism contained in a variable area transect is described. Estimators of density and variance are derived for both randomly distributed and aggregated populations. For randomly distributed populations exact confidence intervals are available. On an effort-precision criterion the method is more useful than other spatial distribution based density estimators. Under the condition where effort is a linear function of distance covered and numbers of organisms counted, the effort expended in achieving a desired level of precision is the same as that for quadrats; the variance of effort depends on the difficulty in counting and in covering the distance. An example using pismo clams (*Tivela stultorum*) is given: the density of clams was found to be 1 per 2.87 m². The method was found to be superior to that of other distance-measures and quadrats.

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Two methods are commonly employed when measuring the density of plant communities and closed animal populations where the animals are relatively stationary: quadrats and distance-measures. Quadrats are simple to apply. The fact that means of plot samples provide an unbiased estimate of true mean density enhances the usefulness of quadrats. Unfortunately, problems arise in quadrat sampling. Quadrats of different size yield different estimates of density (Greig-Smith 1964). Also, the degree of nonrandomness detected depends on plot size (Pielou 1957). Distance-measure methods, where the density is based on the spatial distribution of organisms, avoid these difficulties. The density estimate is based on the distance between some randomly chosen point and some r th closest organism and not on a fixed plot.

Unfortunately, there are also problems in using distance-measures. The precision of the estimate is inverse to the product of the number of samples taken, n , and the number in each sample, r (Pollard 1971). In the field, an r beyond 3 or 4 is often impractical. This difficulty arises not from the measurement to the r th organism but in determining which is the r th. Increased precision is afforded only

at the expense of increasing the number of sample points. This has discouraged many investigators from using distance-measures.

One way to avoid the difficulties of quadrats and distance-measures is to sample in such a way that the search for the r th organism is a consequence of traversing a transect. In this way searching and measuring the distance are accomplished at the same time. A large sample size is easily obtained and the estimate is still free of the restrictions imposed by a fixed plot size.

The author would like to thank L. L. Eberhardt for his suggestions in the original formulation of the problem and D. G. Chapman for his suggestions, especially those on the comparison of methods. Personnel from the California Department of Fish and Game participated in data collection.

ESTIMATION

Maximum Likelihood Estimation of Density

Consider the following: A resource management biologist proceeds along a transect of constant and fixed width, w , until he reaches the r th organism. If the

organisms are Poisson randomly distributed with constant density, the probability of r or more organisms being contained in a plot of area, w , where x is the measure of distance to the r th organism, is

$$F_r(x) = \sum_{i=r}^{\infty} (\lambda wx)^i \exp(-\lambda wx) / i! \quad (1)$$

The density function, upon differentiating with respect to x , is

$$F_r(x) = (\lambda w)^r x^{r-1} \exp(-\lambda wx) / (r-1)! \quad (2)$$

If we have $x_1, x_2, \dots, x_n$ sample distances from n sample point then the modified (unbiased) maximum likelihood estimator of the density is (see Appendix, Part A)

$$\hat{\lambda} = \frac{nr - 1}{w \sum_{i=1}^n x_i} \quad (3)$$

where the variance is

$$\text{var } \hat{\lambda} = \frac{\lambda^2}{nr - 2} \quad (4)$$

For the variance to be finite the product nr must be greater than 2.

Confidence Intervals

Often an investigator is interested in knowing not only an estimate of the density but also an interval of confidence in which it is expected to occur. Equation (2) is used to derive the characteristic function of x which is used to construct an exact confidence interval for the density. The characteristic function is unique for any distribution. Thus, for a given density function the characteristic function can be used to index the underlying distribution. Once the underlying distribution is known the confidence interval can be readily identified as will be presently shown.

By definition, the characteristic function of x the distance to the r th organism, is the expected value of $\exp(itx)$, i.e.,

$$\phi_x(t) = E[\exp(itx)]$$

which from equation (2) is

$$\begin{aligned} &= \int_0^{\infty} \frac{(\lambda w)^r}{(r-1)!} x^{r-1} \\ &\quad \cdot \exp[-x(\lambda w - it)] dx \\ &= (1 - it/\lambda w)^{-r}. \end{aligned} \quad (5)$$

The characteristic function for the chi-square distribution with m degrees of freedom (df) is

$$\phi(t) = (1 - it)^{-m/2}.$$

Thus from equation (5), $2\lambda wx$ is chi-square distributed with $2r$ df and since the sum of a chi-square is a chi-square with df added $2\lambda w n \bar{x}$ is chi-square with $2nr$ df. This statistic can be used to construct a confidence interval about λ .

For a $1 - \alpha$ percent confidence interval

$$\Pr(C_1 \leq 2\lambda w n \bar{x} \leq C_2) = 1 - \alpha$$

or

$$\Pr(C_1/2wn\bar{x} \leq \lambda \leq C_2/2wn\bar{x}) = 1 - \alpha, \quad (6)$$

where C_1 and C_2 are the lower and upper $\alpha/2$ percentage points from a chi-square distribution with $2nr$ df.

COMPARISON OF METHODS

Variable Area Transect and Closest-Individual

The variance of the modified maximum likelihood estimator is the same for the variable area transect (equation 2) and the closest-individual method (Pollard 1971):

$$\text{Var}(\lambda) = \lambda^2(nr - 2). \quad (7)$$

Under the same sampling conditions an

equal amount of effort is expended in locating n random sample points for both methods. So, in deciding which method requires the least effort to attain a given sample size, and hence, variance, the relative difficulty in measuring r should be examined.

For the closest-individual method, an r beyond 3 or 4 is often impractical; the difficulty arises from determining which organism is the r th. If the investigator searches either in increasing circles or works back and forth across the sample area, a great deal of time and effort is expended. Only when the r th organism can be determined from the sample point does the closest-individual method require little searching effort.

For the variable area transect the determination of the r th organism is a consequence of traversing the transect. Less effort is likely to be expended in determining the order of organisms. Consequently, in most field applications searching effort should be less.

Difficulties might arise in determining transect boundaries. In some situations these boundaries could be laid out as with quadrats, 3 of the sides being fixed with the 4th being variable. Practical alternatives would depend on the terrain. In some situations the investigator could carry a rod and allow the ends of the rod to determine the side boundaries. In any event, the transect should be narrow enough so that it is easy to determine whether or not an organism lies inside the transect boundaries.

Variable Area Transect and Quadrats

In terms of the amount of effort expended in achieving a desired level of precision, the variable area transect and quadrats can be compared under 2 conditions: (1) the major portion of effort is

expended in the examination of the area for specimens and not in either determining boundaries or locating sample points, and (2) the effort invested is assumed to be a linear function of the distance covered and the number of organisms counted.

Under the first condition, Holgate (1964) shows a natural way to compare quadrats and the closest-individual method. This reasoning can be extended to variable area transects as well.

The variance of the density estimator, say $\hat{\lambda}$, for quadrats is

$$\text{Var}(\hat{\lambda}) = \lambda/a \quad (8)$$

where a is the total area sampled.

For the variable area transect the total expected area for n samples can be derived from equation (2):

$$\begin{aligned} E(a) &= nwE(x) \\ &= nw \int_0^\infty (\lambda w)^r x^r \exp(-\lambda wx)/(r-1)! \\ &= nr/\lambda. \end{aligned}$$

Substituting $E(a)$ for a in equation (8),

$$\text{Var}(\hat{\lambda}) = \lambda^2/nr, \quad (9)$$

and since from equation (4)

$$\text{Var}(\hat{\lambda}) = \lambda^2/(nr-2)$$

the variance of a quadrat estimator is smaller. However, for large sample sizes the variances can be assumed to be nearly equal.

Under the second set of conditions we weigh whether less effort is required either to count a random number of organisms over a fixed area or to determine the area for a fixed number of organisms.

Let the following linear relationship describe effort:

$$\begin{aligned} \text{effort} &= d \cdot (\text{distance covered}) \\ &\quad + b \cdot (\text{number counted}), \end{aligned}$$

where d and b are arbitrary constants reflecting the difficulty in covering the distance and in counting the organisms, respectively.

If $E(T_1)$ is the expected effort for the variable area transect then:

$$E(T_1) = dnE(x) + b(nr) \\ = drn/(\lambda w) + b(nr). \quad (10)$$

If $E(T_2)$ is the expected effort for quadrats then

$$E(T_2) = da/w + bE(k) \\ = da/w + b\lambda a, \quad (11)$$

where k is the number counted.

For convenience, letting the width, w , equal unity and the area, a , equal nr/λ , the expected efforts are equal:

$$E(T_1) = E(T_2) = nr(d/\lambda + b). \quad (12)$$

Since effort as defined here is subject to statistical error, we should also investigate its variance.

The variance of T_1 is

$$\text{Var}(T_1) = d^2\text{var}(x) + 0. \quad (13)$$

The variance of x is

$$\text{Var}(x) = [E(x)]^2 - [E(x^2)] \\ = nr/(\lambda w)^2, \quad (14)$$

and therefore

$$\text{Var } T_1 = d^2nr/(\lambda w)^2. \quad (15)$$

The variance of T_2 is

$$\text{Var}(T_2) = 0 + b^2\text{var}(k) = b^2\lambda a \quad (16)$$

since k is a Poisson random variable.

Again, letting w equal unity and $a = nr/\lambda$,

$$\text{Var}(T_1) = d^2nr/\lambda^2, \quad (17)$$

$$\text{Var}(T_2) = b^2nr. \quad (18)$$

The variances are equal when

$$\lambda = d/b. \quad (19)$$

Without prior knowledge of the area to be sampled it is difficult to assign relative values to b and d . However, we can consider 2 cases where a comparison is easily made.

If counting is difficult, relative to that in covering the distance ($b > d$) and if the population is dense, then the variable area transect should have the least variance of effort. So, in this situation, the variance of effort would be more consistent using the variable area transect.

In the opposite situation, where the distance is difficult to cover relative to the difficulty in counting the organisms, $d > b$, and the density is low, quadrats offer the effort of least variance.

AN EXAMPLE

Pismo clams (*Tivela stultorum* Mawe) inhabit open sandy beaches from the intertidal zone to beyond the surf line. The density of clams on the portion of the beach utilized by recreational clam diggers is valuable management information.

The following example is from data collected at Seal Beach, California, during the midday low tide of 16 February 1977. Transect lines were laid from randomly selected points on the exposed beach. Along the lines, the beach was probed with a 6-prong clamming fork until the 3rd clam was reached. Because of heavy surf an r greater than 3 was not practical.

The width of the fork, 0.23 m, is the transect width. The measured distances to the 3rd clam are listed in Table 1. Fourteen samples were taken.

The sum of distances to the 3rd clam is

$$\sum_{i=1}^{14} x_i = 510.8.$$

Since $nr = 42$, the density estimate from

Table 1. The distance from a randomly chosen point to the third organism, X_i , in meters. The Z statistic and the empirical distribution function, S_n , used for testing the hypothesis of randomness.

X_i	5.4	15.3	33.2	7.8	43.0	60.5	49.8	63.4	42.3	35.8	65.8	15.3	13.9	59.3
Z_i	0.07	0.14	0.21	0.28	0.36	0.42	0.50	0.57	0.64	0.71	0.78	0.85	0.92	1.00
S_n	0.01	0.04	0.11	0.12	0.21	0.32	0.42	0.55	0.63	0.72	0.83	0.86	0.88	1.00

equation (3) is $\lambda = 0.35/\text{m}^2$ or 1 clam per 2.87 m^2 .

The lower and upper 0.025 percentage points from a chi-square distribution with $2nr = 84$ df are $C_1 = 60.5$, $C_2 = 111.2$. Hence, from equation (7) the 95% confidence limits are [0.26, 0.47] clams per square meter. The confidence interval is skewed because it is based on the chi-square distribution.

The statistic Z_j , where

$$Z_j = \sum_{i=1}^j x_i / \sum_{i=1}^{14} x_i,$$

is an ordered statistic from the uniform distribution on the interval (0, 1) (Seshadri, Csorgo, and Stevens 1969) and can be used to test the hypothesis of randomness. The Z_j and the empirical distribution $S_n (=j/n)$ are listed in Table 1. The supremum of 0.15 is well below the critical value of 0.349 (from Owen 1962) for the 1 sample Kolmogorov-Smirnov test and the hypothesis of randomness cannot be rejected at the 0.05 level.

In this example it probably would not have been as practical to use the closest-individual method. Because waves constantly washed over the sampling area it would have been difficult to determine exactly what areas had been sampled. Resampling, and consequently wasted effort, would have been difficult to avoid.

There was some difficulty in counting because the clams had to be dug to be identified. The distance was relatively easy to cover since there were no obstacles on the exposed beach. Therefore, the variable area transect offered advantages

over using quadrats. However, had the surf been heavier and more troublesome to covering the distance, quadrats would probably have been more advantageous.

This example helps to illustrate several points about the theoretical framework of the model and its applications. The precision of the method is not enhanced by inclusion of the distance measures to the 1st and 2nd organisms. Because the organisms are modeled as being randomly distributed the information content of the measurements to the 3rd organism contains all the information expressed by those distances to the 2nd and 1st. Note that while the number of measurements is n , the variance, equation (4) is inverse to the total number encountered, the product nr .

If the density is zero the variable area transect method will be of no value because the density estimate, equation (3), is dependent on at least 1 measure of distance. For the density to be zero, the distance, the denominator of equation (3), must be infinity. In this case quadrats would be superior to the variable area transect because for quadrats the variable being measured, the number of organisms, is in the numerator of the assembly equation and can be zero. Investigating the area beforehand for organisms can eliminate this problem.

The clams were assumed to be of uniform density over the entire area sampled. Because a significant deviation from randomness could be used as evidence to the contrary and because no such deviation was found, the assump-

tion is probably true. This is most likely because the exposed area of the beach is relatively flat, making the environment homogeneous to life-supporting and life-damaging influences. However, it is not difficult to imagine that beyond the surf line, where inundation and protection from clam harvesting is greater, the density is higher than that of the exposed beach. The density could also change along the beach. Substrate, angle of wave action, and utilization by clam diggers cannot be thought of as being invariant over the entire stretch of the beach. For the situation where distinct areas of different densities can be defined, an estimator is described in the following section. When distinct areas are not easily defined difficulties can arise. It would probably be best for the investigator to define the areas as well as possible and then proceed. If the investigator does not have some prior knowledge about the interaction of organisms and terrain then some presampling may be appropriate.

DENSITY ESTIMATOR FOR RANDOM AND CLUSTERED DISTRIBUTIONS

An alternative to randomness often encountered in biological problems is that of aggregation, or heterogeneity. A special case of aggregation occurs when a population is divided into distinct regions of different densities, where the organisms are randomly distributed within each region. For the closest individual method Morisita (1957) proposes an unbiased estimator of density for this situation. For the variable area transect the analog to Morisita's estimator is (see Appendix, Part B)

$$\hat{\lambda} = \frac{(r-1) \sum_{i=1}^n x_i^{-1}}{nw} \quad (20)$$

or

$$\hat{\lambda} = \frac{\sum_{i=1}^n \hat{\lambda}_i}{n},$$

where $\hat{\lambda}_i$ is the density defined for each sample point. It can be shown that $\hat{\lambda}_i$ is unbiased for the random distribution described in equations (1) and (2) with the following variance (see Appendix, Part B)

$$\text{Var}(\hat{\lambda}) = \frac{\lambda^2}{n(r-2)}, \quad (21)$$

which has an unbiased replicated sample estimate

$$\text{Var}(\hat{\lambda}) = \frac{\sum (\hat{\lambda}_i - \hat{\lambda})^2}{n(n-1)}. \quad (22)$$

Thus when the population is uniformly random over the area sampled there are 2 density estimators: $\hat{\lambda}$, equation (3) and $\hat{\lambda}_i$, equation (20). Since the variance is always less for $\hat{\lambda}$, $(nr-2)$ always being greater than $n(r-2)$, it would be preferable to use $\hat{\lambda}$ over $\hat{\lambda}_i$ in this situation.

For the situation where the densities are variant for different regions the sampling must be done from random points within each region. Also, a separate test of randomness should be carried out for each region.

The negative binomial distribution is often used to model aggregated populations. Parker (1976) shows that $\hat{\lambda}$ is unbiased for the negative-binomial distribution with the following variance:

$$\text{Var}(\hat{\lambda}) = \frac{\lambda^2}{n(r-2)} \left[1 + \frac{n(r-1)}{k} \right]. \quad (23)$$

Two parameters must be estimated: λ , the density and k , the heterogeneity parameter. In discussing Morisita's estimator, Eberhardt (1967) noted that k will tend to vary with r . This is also the case for equation (23); for a given variance k must change with r . Consequently, the negative binomial model may not be en-

tirely realistic for distance-measure methods. If an investigator suspects aggregation, in the sense that it cannot be divided into distinct regions of randomness, he is advised to use the quadrat methods as outlined by Bliss and Fisher (1953).

DISCUSSION

For density estimation an investigator is usually interested in a method which is accurate, precise, and requires minimum field effort. When organisms are distributed at random (Poisson) the variable area transect offers a useful alternative to other distance-measures methods, and quadrats. For small sample sizes the variable area transect should be especially useful because the confidence intervals are exact.

Both the variable area transect and closest-individual methods provide unbiased estimates of density with equal variances. The relative effort expended in achieving a desired sample size should be less for most sampling situations with the variable area transect because determining the order of organisms could likely require less searching effort than with the closest-individual method.

Both quadrats and variable area transects can be used for unbiased density estimation under the condition of randomness. For an equal sampling area the variance for quadrats is slightly less. When effort is a linear function of distance covered and number counted, both methods require an equal sampling effort. When counting is difficult and the population is dense, the effort is more consistent for the variable area transect. When the density is low and the distance is difficult to cover, the effort is more consistent for quadrats.

A density estimator can be derived that

is useful for both uniformly random populations and aggregated populations, where the variant density for different regions is randomly distributed. The estimator is unbiased for the negative binomial distribution as well, the implication being that the estimator is robust for a wide set of conditions as yet undefined.

In conclusion, the variable area transect provides a useful sampling alternative. Because of ease of operation and because the resulting estimate is free of quadrat size, the variable area transect should be useful in a wide range of biological sampling problems.

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APPENDIX A. MAXIMUM LIKELIHOOD ESTIMATION OF DENSITY

The maximum likelihood estimator is that which maximizes the likelihood that a set of distance measures $x_1, x_2, \dots, x_n$ assume a particular value given the density function of the population density. Maximum likelihood estimators are appealing to use because they are asymptotically efficient, normal, and unbiased.

From the density function, equation (2), the likelihood function is

$$L(\lambda) = \left[(\lambda w)^{nr} (x_1^{r-1} \cdot x_2^{r-1} \cdot \dots \cdot x_n^{r-1}) \cdot \exp\left(-\lambda w \sum_{i=1}^n x_i\right) \right] / [(r-1)!]^n.$$

Taking the partial derivative with respect to λ , equating to 0 and solving for λ the maximum likelihood estimator is

$$\hat{\lambda} = nr / \left(w \sum_{i=1}^n x_i \right).$$

As a check for bias, the expected value of $\hat{\lambda}$ is

$$E(\hat{\lambda}) = \int_0^\infty \dots \int_0^\infty \frac{nr}{w \sum_{i=1}^n x_i} \prod_{i=1}^n \frac{(\lambda w)^r x_i^{r-1} \exp(-\lambda w x_i)}{(r-1)!} dx_i. \quad (A1)$$

By making the following transformation integration of equation (A1) is simplified:

$$U_j = \sum_{i=1}^j x_i.$$

U_n is integrated from 0 to ∞ , and each U_j is integrated from U_j to U_{j+1} . The first $n-1$ integrals are beta, the last is a gamma:

$$E(\hat{\lambda}) = \frac{nr}{nr-1} \lambda.$$

Although asymptotically unbiased, $\hat{\lambda}$ is biased for small sample sizes. From the invariance principle of maximum likeli-

hood estimators, the modified (unbiased) maximum likelihood estimator is

$$\hat{\lambda} = \frac{(nr-1)}{nr} \cdot \frac{nr}{w \sum_{i=1}^n x_i} = \frac{nr-1}{w \sum_{i=1}^n x_i}.$$

To estimate the variance of $\hat{\lambda}$ the second moment of $\hat{\lambda}$ is computed with the same transformations as above, where

$$E(\hat{\lambda}^2) = \frac{(nr-1)}{(nr-2)} \lambda^2,$$

and then the variance of $\hat{\lambda}$ is, from definition,

$$\text{Var}(\hat{\lambda}) = E(\hat{\lambda}^2) - [E(\hat{\lambda})]^2 = \frac{\lambda^2}{(nr-2)}.$$

APPENDIX B. EXPECTATION AND VARIANCE OF GENERAL ESTIMATOR

Eberhardt (1967) showed that the expected value of the reciprocal of the measure of distance to the r th organism is equivalent to Morisita's (1957) estimator. The situation is the same with the variable area transect. From equation (2)

$$E(x^{-1}) = \frac{(\lambda w)^r}{(r-1)!} \int_0^\infty x^{r-2} \exp(-\lambda w x) dx = \frac{\lambda w}{r-1},$$

and then an estimate of the density is

$$\hat{\lambda} = \frac{(r-1)E(x^{-1})}{w}.$$

As a test for bias

$$E(\hat{\lambda}) = \int_0^\infty \dots \int_0^\infty \frac{(r-1) \sum_{i=1}^n x_i^{-1}}{nw}$$

$$\cdot \prod_{i=1}^n \frac{(\lambda w) x_i^{r-1} \exp(-\lambda w x_i)}{(r-1)!} dx_i,$$

which can be solved directly without transformations:

$$E(\hat{\lambda}) = \lambda.$$

The 2nd moment is derived similarly where

$$E(\hat{\lambda}^2) = \frac{\lambda^2 + \lambda^2 n(r-2)}{n(r-2)}$$

and the variance is

$$\begin{aligned} \text{Var}(\hat{\lambda}) &= E(\lambda^2) - [E(\lambda)]^2 \\ &= \frac{\lambda^2}{n(r-2)}. \end{aligned}$$

Movements of Pelagic Dolphins (*Stenella* Spp.) in the Eastern Tropical Pacific as Indicated by Results of Tagging, With Summary of Tagging Operations, 1969-76

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ABSTRACT

Through 1976, 3,712 small cetaceans were tagged in the course of research cruises operating out of the Southwest Fisheries Center. These included 2,996 spotted dolphins, *Stenella attenuata*; 324 spinner dolphins, *S. longirostris*; 193 common dolphins, *Delphinus delphis*; and 113 bottlenose dolphins, *Tursiops truncatus*. Others tagged in small numbers included Pacific whitesided dolphins, *Lagenorhynchus obliquidens*; striped dolphins, *Stenella coeruleoalba*; and a short-finned pilot whale, *Globicephala macrorhynchus*. Several types of tags were used. Tags have been recovered from 97 spotted dolphins and 7 spinner dolphins. Time at liberty ranged from less than 2 h to more than 4 yr. Net distance traveled ranged from 7 to 582 n.mi. Average short-term movement in the spotted dolphin is 30-50 n.mi./day; range is 200-300 n.mi. in diameter, and seasonal onshore-offshore migrations may exist.

INTRODUCTION

Populations of pelagic dolphins are important to the purse seine fishery for yellowfin tuna in the eastern tropical Pacific and are affected by the fishery.³ Adequate assessment of the impacts of the fishery on the dolphin populations requires knowledge of such aspects of life history as home range and seasonal migration. For this reason, we began a program of tagging dolphins in 1969. The tagging program was specifically designed to examine movements, but the tagging itself was largely opportunistic. In addition, research projects with other objectives but involving tagging have also yielded information on movements. The main purpose of this report is to summarize and to report the results of analyses of data on movements of spotted dolphins, *Stenella attenuata*, and spinner dolphins, *S. longirostris*, yielded by tag returns through 1976. A secondary purpose is to summarize and document all dolphin tagging operations carried out in conjunction with dolphin/tuna research at the Southwest Fisheries Center, La Jolla, Calif., from 1969 through 1976. This is necessary because of the possibility that tagged dolphins released by us may be recovered by other investigators not familiar with our program. We suspended field work in our tagging program in 1976, pending development of better tags and design of a plan for large-scale tagging aimed at estimating population sizes. The results of the expanded program will be the subject of future reports.

Many small marine odontocetes are thought to undergo migrations of varying scale in time and distance. Most published conclusions about movements have been based on sightings or strandings and have to do with season of the year or sea surface temperature. Fraser (1934) noted a possible intrusion of elements of the warm-temperate Atlantic cetacean fauna (including *Delphinus delphis*) into the North Sea during a year of anomalous sea-surface warming. Sightings and correlated oceanographic data suggest that the distributions of dolphins (*Lissodelphis peroni*, *Lagenorhynchus cruciger*, *Lagenorhynchus obscurus*, and *Delphinus delphis*) off the east coast of New Zealand are "closely associated with certain temperature ranges and consequently with specific water masses and convergence regions," causing different animals to be seen in summer than in winter (Gaskin 1968). Similarly, Kasuya (1971) found, on the basis of aerial sightings, that warm-water delphinids, including *Stenella attenuata*, in Japanese waters migrate north in the summer season as far as Hokkaido; whereas cold-water forms, such as *Phocoenoides dalli* and *Lissodelphis borealis*, migrate south in the winter. The northern extent of the distribution of the warm-water forms may vary seasonally as much as 13° of latitude (780 n. mi.) (Miyazaki et al. 1974). Evans (1975) demonstrated the existence of similar seasonal migrations by the common dolphin, *D. delphis*, off the coasts of southern California and Baja California. Several other similar studies have been carried out, and this review is not exhaustive.

Very little information has been available on home range of pelagic dolphins. As Norris (1967) noted, some dolphins seem quite sedentary. He found that herds of spinner dolphins, *Stenella longirostris*, are consistently found off limited stretches of coast; five such home ranges have been tentatively recognized off Oahu, Hawaii. On the other hand, some other dolphins are very

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³Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Pacific Yellowfin Tuna Fishery. Unpubl. Manuscr., 109 p. SWFC Admin. Rep. No. LJ-76-29, Nat. Mar. Fish. Serv., La Jolla, CA 92038.

mobile. Herds of common dolphins off southern California and Baja California may move as far as 120 km in a 24-h period, following underwater escarpments (Evans 1971, 1974).

Preliminary results of our tagging program through early 1974 have been previously published (Perrin 1975). Time at liberty for tagged spotted dolphins ranged from 1.7 h to 502 days and minimum distance traveled from 13 to 532 km.⁴ The tentative conclusion was that these data indicate a great deal of east-west and north-south movement within the eastern portion of the range of the off-

shore race of *S. attenuata*. Tag returns for *S. longirostris* showed less net movement.

MATERIALS AND METHODS

During the course of research on the dolphin/tuna problem, 3,712 small cetaceans were tagged (Table 1), including 2,996 spotted dolphins (Fig. 1) and 324 spinner dolphins (Fig. 2). One of us (Evans) carried out other dolphin-tagging operations during the period 1969-76, but these did not involve *Stenella* spp. and will be described in another report. Several types of tags and tag legends were used:

1. *Spaghetti tag with plastic dart*. This tag was described and figured by Nishiwaki et al. (1966). The

⁴A maximum value for minimum distance traveled of 2,415 km was given in Perrin (1975). Subsequently, additional information has been acquired concerning the recapture of that tag, and the data are now considered to be unreliable and are not included in the analysis below.

Table 1.—Dolphins and small whales tagged, 1969-76. Radiotags included.

Year	<i>Stenella attenuata</i>	<i>Stenella longirostris</i>	<i>Delphinus delphis</i>	<i>Tursiops truncatus</i>	Other	Unidentified	Total
1969	207	11	0	0	0	0	218
1970	618	94	10	0	0	146	768
1971	147	18	50	12	21	15	243
1972	306	41	28	19	27	0	401
1973	203	35	56	8	42	1	305
1974	1,048	70	23	72	27	1	1,221
1975	336	46	26	2	44	2	416
1976	131	9	0	0	0	0	140
Total	2,996	324	193	113	21	65	3,712

¹Probability is high that these were either spotted dolphins, *Stenella attenuata*, or spinner dolphins, *S. longirostris*.

²Pacific white-sided dolphin, *Lagenorhynchus obliquidens*.

³Spotted or spinner dolphins.

⁴Striped dolphin, *Stenella coeruleoalba*.

⁵Two striped dolphins and two short-finned pilot whales, *Globicephala macrorhynchus*.

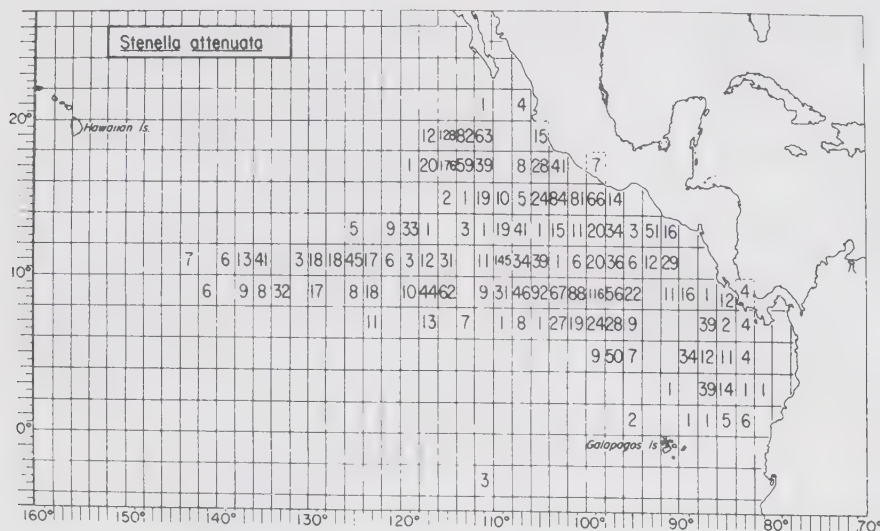


Figure 1.—Number of releases of tagged spotted dolphins, *Stenella attenuata*, by 2-degree area, 1969-76. Releases given in Table 1 for which precise localities are not available are not included.

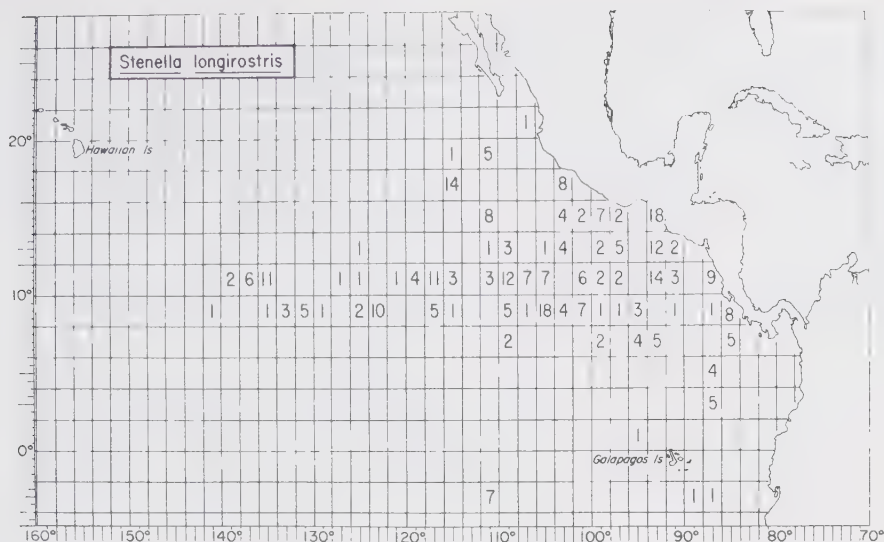


Figure 2.—Number of releases of tagged spinner dolphins, *Stenella longirostris*, by 2-degree area, 1969-76. Two dolphins given in Table 1 for which precise localities are not available are not included.

tags released in 1969 and 1970 were yellow and bore one of two legends (in addition to serial number):

- a. RETURN TUNA COMM SAN DIEGO or
- b. REWARD BU COMM FISHERIES SAN DIEGO.

2. *Spaghetti tag with steel dart.* This type of tag was developed for use on large pelagic fishes (Mather 1963) and was first used on cetaceans by Sergeant and Brodie (1969). It has been modified from its original design by addition of a clear plastic sleeve to protect the legend (Evans et al. 1972). It is manufactured by Floy Tag and Manufacturing, Inc., Seattle, Wash. Four versions of the tag were used in the operations described here:

- a. 15-cm long, orange, with legend:
REWARD U.S. BUR COMM FISH LA JOLLA,
CALIF(CF)
- b. 12-cm long, yellow, with legend:
REWARD NATL MARINE FISH SERVICE LA
JOLLA, CAL
- c. 32-cm long, yellow, with legend:
NUC-502 SAN DIEGO, CAL. 92132 REWARD
- d. 30-cm long, orange, with legend:
NATIONAL MARINE FISHERIES SERVICE
LA JOLLA, CA U.S.A. REWARD.

3. *Spaghetti tag with steel dart/braided.* These tags were designed at sea for use in underwater observations of tagged dolphins during the research cruise of the *Elizabeth C. J.* in 1976 (see following section on Chronological Account of Tagging Operations, 1969-76). Three-strand braids of spaghetti tubing of various colors were linked together in unique color/length com-

binations and fastened to steel-dart tags from which all but 1 in of tubing (bearing the serial number) has been removed. Six-inch lengths of 1/2-in wide flexible, bright orange plastic streamers were added to the ends of some of the tags to further increase visibility.

4. *Plastic deer ear tag.* This tag ("jumbo rototag") was described and figured by Norris and Pryor (1970). Tag and applicators are manufactured by Dalton, Henley, United Kingdom.

- a. Tags released in 1971 were yellow and bore the legend:

DEVUELVA OF. DE PESCA PREMIO. 150
PESOS BU COMM FISH SAN DIEGO CON
CABEZA

- b. Tags released in 1972 were yellow, with the legend:

\$15 DOLLAR REWARD FOR RETURN WITH
HEAD BU COM FISH SAN DIEGO

- c. Tags released in 1973 were white and bore no legend other than the serial number.

5. *Radiotag.* Martin et al. (1971) and Evans (1971, 1974) described and figured the radiotags used.

CHRONOLOGICAL ACCOUNT OF TAGGING OPERATIONS, 1969-76

1. In 1969 and 1970, the Inter-American Tropical Tuna Commission (IATTC) conducted tuna-tagging operations on three cruises on the chartered tuna seiners, the *Connie Jean* and the *Anne M.* At NMFS' request, tuna tags (spaghetti tag with plastic dart—see discussion of tag types above) were also placed in dol-

phins captured with tuna (see Bayliff 1973 for description of tagging operations). Nine hundred and forty-nine dolphins were thusly tagged (Table 2).

2. In 1970, a crewman on the seiner *Conquest* volunteered to tag dolphins during fishing operations. He tagged 37 dolphins (probably spotted and spinner dolphins) with plastic-dart spaghetti tags.

3. Beginning in 1971, scientific observers from NMFS each year have accompanied some tuna seiners to the "porpoise-fishing" grounds. Through 1975, these observers tagged dolphins on an opportunity basis. The observers tagged 105 dolphins on 3 cruises in 1971, 316 on 9 cruises in 1972, 204 on 16 cruises in 1973, 1,221 on 25 cruises in 1974, and 416 on 22 cruises in 1975 (Table 3). Two short-finned pilot whales,

Table 2.—Tags released from commercial seiners, 1969-76. Releases by NMFS observers aboard nonchartered seiners are detailed in Table 3. Tag type PD = plastic-dart spaghetti tag, MD = metal-dart spaghetti tag (see Table 3), DE = deer ear tag, and RX = radio-transmitter tag. Letters a, b, and c refer to tag type subcategories defined in text.

Vessel	Cruise number	Cruise period	Tagged						Total	Tag type
			Spotted dolphin	Spinner dolphin	Common dolphin	Bottlenosed dolphin	Other	Unidentified		
<i>Connie Jean</i>	1055	Oct-Nov 69	207	11	0	0	0	0	218	PD (a)
<i>Anne M</i>	1057	Jun-Aug 70	≥278	≥46	10	—	—	9	343	PD (61a, 278b)
<i>Anne M</i>	1058	Sep-Nov 70	340	48	0	0	0	0	388	PD (b)
<i>Conquest</i>	—	Mar-Apr 70	—	—	—	—	—	37	37	PD (b)
<i>Queen Mary</i>	13	Nov-Dec 71	≥105	—	0	0	0	15	120	MD (107b, 24c)
			15	0	0	0	0	0	15	DE (a)
			3	0	0	0	0	0	3	RX
<i>Independence</i>	26	Sep-Oct 72	1	4	18	0	21	0	24	MD (a)
			61	0	0	0	0	0	61	DE (b)
<i>Trinidad</i>	52	Oct-Nov 73	12	1	7	0	0	0	20	MD (a)
<i>John F. Kennedy</i>	53	Nov-Dec 73	59	0	0	0	0	0	59	MD (a)
			22	0	0	0	0	0	22	DE (c) ³
<i>Elizabeth C J</i>	208	Oct-Dec 76	124	8	0	0	0	0	132	MD ⁴
			7	1	0	0	0	0	8	RX
Total			1,234	119	35	0	1	61	1,450	

¹Spotted or spinner.

³With 2-in disc.

²Pacific white-sided dolphin, *Lagenorhynchus obliquidens*.

⁴With braided tubing.

Table 3.—Tag releases (steel-dart spaghetti tags) by NMFS observers aboard commercial tuna seiners, 1971-75. Tag types defined in text.

Cruise number	Year	Tagged						Totals	Tag type
		Spotted dolphin	Spinner dolphin	Common dolphin	Bottlenose dolphin	Other	Unidentified		
6	1971	0	0	23	0	11	0	24	(a)
8		8	18	17	11	0	0	54	(a)
9		16	0	10	1	0	0	27	105 (10c, 95a)
14	1972	18	0	0	0	0	0	18	(a)
15		43	0	2	0	0	0	45	(a)
16		22	21	0	0	0	0	43	(a)
17		6	0	2	9	16	0	23	(a)
20		16	0	0	0	0	0	16	(a)
21		54	1	0	1	0	0	56	(a)
22		32	13	0	0	0	0	45	(a)
23		15	0	0	0	0	0	15	(a)
24		38	2	6	9	0	0	55	316 (a)
29	1973	2	4	7	0	0	0	13	(a)
30		12	5	0	0	0	1	18	(a)
31		1	0	0	0	0	0	1	(a)
32		1	0	0	0	0	0	1	(a)
33		1	0	0	0	0	0	1	(a)
34		9	0	0	0	0	0	9	(a)
38		4	1	0	0	0	0	5	(a)
39		1	0	0	0	0	0	1	(a)
40		1	0	0	0	0	0	1	(a)
41		12	10	6	0	0	0	28	(a)
43		5	1	4	0	0	0	10	(a)
44		11	1	4	0	22	0	18	(a)
45		23	0	8	0	0	0	31	(a)
47		7	0	4	0	0	0	11	(a)
48		9	12	16	8	0	0	45	(a)

Table 3.—Continued.

Cruise number	Year	Spotted dolphin	Spinner dolphin	Common dolphin	Tagged			Uniden- tified	Totals	Tag type
					Bottlenose dolphin	Other				
49	1974	11	0	0	0	0	0	11	204	(a)
54		0	3	0	0	0	0	3		(a)
55		3	0	0	0	0	0	3		(b)
57		16	3	0	0	0	0	19		(a)
58		47	3	0	9	0	0	59		(a)
59		24	8	2	4	0	0	38		(a)
61		51	8	4	17	13	0	83		(b)
65		17	0	4	0	0	0	21		(a)
66		29	0	0	0	0	0	29		(a)
67		0	1	0	0	0	0	1		(a)
68		20	1	7	0	0	0	28		(b)
71		2	5	0	0	0	0	7		(a)
72		1	0	0	0	0	0	1		(b)
73		3	2	0	0	0	0	5		(a)
74		34	1	0	0	0	1	36		(b)
75		2	0	0	0	0	0	2		(a)
76		1	1	0	0	0	0	2		(a)
78		8	0	0	0	0	0	8		(b)
80		10	0	0	0	0	0	10		(a)
81		2	0	0	8	0	0	10		(b)
82		34	0	0	0	0	0	34		(a)
87		91	5	6	32	14	0	138		(b)
90		5	7	0	0	0	0	12		(a)
91		623	14	0	2	0	0	639		(a)
94		5	2	0	0	0	0	7		(a)
96		20	6	0	0	0	0	26	1,221	(a)
99	1975	1	0	0	0	0	0	1		(a)
100		16	0	0	1	0	0	17		(d)
102		43	2	0	0	21	0	46		(d)
104		42	4	0	0	0	32	48		(d)
105		18	2	0	0	0	0	20		(d)
106		45	3	0	1	0	0	49		(d)
110		3	0	0	0	21	0	4		(d)
112		42	8	0	0	0	0	50		(d)
113		27	10	0	0	0	0	37		(d)
114		1	0	0	0	0	0	1		(d)
115		6	1	0	0	0	0	7		(b)
116		2	1	0	0	0	0	3		(d)
117		1	0	0	0	0	0	1		(d)
118		0	2	0	0	0	0	2		(d)
119		15	5	0	0	0	0	20		(d)
120		1	0	0	0	0	0	1		(d)
121		43	0	0	0	0	0	43		(d)
123		8	1	2	0	42	0	13		(d)
124		1	0	0	0	0	0	1		(d)
125	5	0	0	0	0	0	5		(d)	
129	16	7	24	0	0	0	47	416	(d)	
Total		1,762	205	158	113	20	4	2,262		

¹Pacific white-sided dolphin, *Lagenorhynchus obliquidens*.²Striped dolphin, *Stenella coeruleoalba*.³Spotted dolphin or spinner dolphin.⁴Short-finned pilot whale, *Globicephala macro-rhynchus*.

Globicephala macrorhynchus, were also tagged in 1975. Before application, the tag heads were sprayed with Topazone, a topical antibiotic. The tags were applied in several different ways:

a. from the bow (when animals rode the bow wave), with a quick-release head (Beckett 1968) mounted on a long wooden pole or with a crossbow (as described by Kasuya and Oguro 1972, but using a rubber stop on the crossbow bolt rather than a brass stop);

b. from a skiff at the corkline of the seine during the dolphin-rescue maneuver called "backing-down" (see Perrin 1969 for details of fishing operation), using short (40 cm) wooden wands, with permanently mounted tag pins, as applicators; and

c. on the work-deck, when live dolphins were extricated from the net or the catch and then thrown overboard, using short applicators.

4. In late 1971, NMFS chartered the tuna seiner *Queen Mary* for a dolphin/tuna research cruise on the fishing

grounds. Three tagging operations were carried out on the cruise.

- a. Radiotags were attached to spotted dolphins, to monitor herd movements, herd integrity, and recruitment of associated yellowfin tuna to the herd. The technique has been described by Evans (1971, 1974). Five dolphins were radiotagged and followed.
 - b. Fifteen spotted dolphins were measured, sexed, and injected with lead acetate and tagged with plastic deer ear tags placed in the dorsal fin. The animals were pulled into a small skiff for examination and tagging. Technique of application was described by Norris and Pryor (1970). The purpose of the injection of lead acetate was to lay down a time check in the hard tissues, so that growth rates in teeth and bone could be calibrated through examination of recaptured animals. The technique was developed by Nishiwaki and Yagi (1953). The tagged animals were also injected with an antibiotic to combat sepsis. Results of this experiment will be analyzed when tags are returned (none returned with sufficient data to date).
 - c. One hundred and twenty dolphins were also tagged with steel-dart spaghetti tags.
5. In late 1972, NMFS chartered the seiner *Independence* for a dolphin/tuna cruise. Sixty-one spotted dolphins were injected with lead acetate and tagged with plastic deer ear tags. Tagging was accomplished through use of an aluminum chute supported by two skiffs at the corkline of the seine (Fig. 3). In addition, 24 dolphins were tagged with steel-dart spaghetti tags.
 6. Also in 1973, the seiner *Trinidad* was chartered by NMFS for technological research on dolphin rescue methods and equipment. During the cruise, 20 dolphins were tagged with steel-dart spaghetti tags.
 7. In late 1973, NMFS chartered the seiner *John F. Kennedy*. The main purpose of the cruise was to conduct research on dolphin-rescue methods, but some tagging was also carried out. Twenty-two spotted dolphins in a single herd were tagged with white deer ear tags, inserted in the dorsal fin. A 2-in diameter thin red plastic disc was placed on the tag post on each side of the fin to increase visibility of the tag in the water. The objective was to tag dolphins in several herds, using a different color for each herd, and then to study herd structure and integrity through observation of tagged animals in the seine in subsequent hauls in the same area. Rough weather, however, prevented further use of the tagging chute (described above) and completion of the scheduled tagging. In addition to the 22 dolphins tagged with ear tags, 59 spotted dolphins were tagged with steel-dart spaghetti tags.
 8. In late 1976, NMFS chartered the seiner *Elizabeth C. J.* for a combined dolphin/tuna behavioral research and gear research cruise sponsored by several governmental and private organizations. Two types of tags were used to mark dolphin schools so that they could be followed and recaptured and the tagged dolphins observed in the net. Radiotags were placed on seven spotted dolphins and one spinner dolphin. The radiotags failed after only a few hours, but two were subsequently recovered (the recoveries are treated below like other tag returns; the radio-transmitted data will be presented elsewhere). In addition, 124 spotted dolphins and 8 spinner dolphins were tagged with steel-dart spaghetti tags modified for greater underwater visibility (see 3. *Spaghetti tag with steel dart/braided above*).

ACCOUNT OF RADIOTRACKING EXPERIMENT

Transmitters were placed on one adult male (animal A) and two adult females (animals B and C) captured in a tuna seine on 21 November 1971. The object of the experiment was to track the school and set the net on what was assumed to be the same herd five times, at 24-h intervals and at about 1000. The initial set was in the afternoon, and the tagged animals were not released until almost sunset. The chronology of events (Fig. 4) may be summarized as follows:

After the release of the tagged animals it became increasingly obvious that the behavior of the male was quite different from that of the females. At first all animals appeared to stay on the same relative heading. After sunset the females began to move away from the male and the decision was made to stay with the male. After 6 h of tracking the females were separated from the male by an estimated 12 n.mi. and their transmitted signals were extremely weak. It was assumed the transmitter on at least one of the two animals (B and C) had failed.

The vessel followed the male (A) until 1040 on 22 November when the first recapture set was made (set 2). Net distance traveled between initial release and this recapture was 59 n.mi., in about 16 h. One of the females (C) rejoined the male (A) at 0800 but separated from him again at 0930 prior to the net set. An additional long-range transmitter was placed on another male (D) during set 2. Also, a long-life, short-range transmitter was placed on another female (E). After release, A and D stayed together and were rejoined by one of the females from the first set (C). Female B was not seen again following her separation from A and C after initial release in set 2. A, D, E, and C were followed until 1036 (set 3) on 23 November. Net distance traveled in 24 h was 28 n.mi. During this period, the males (A and D) were separated by some distance (3 n.mi.) from the school containing the females (C and E). The set (3) was made on the portion of the school containing the males A and D. They evaded capture by passing between the boat and the net skiff be-

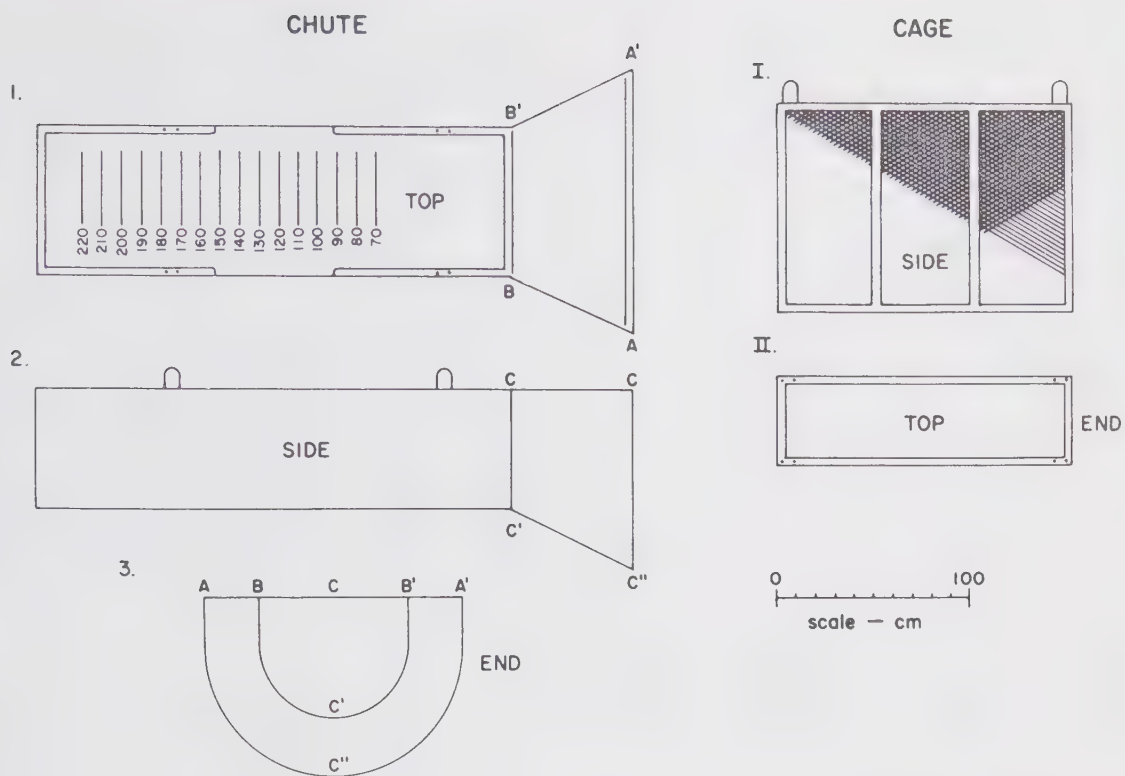
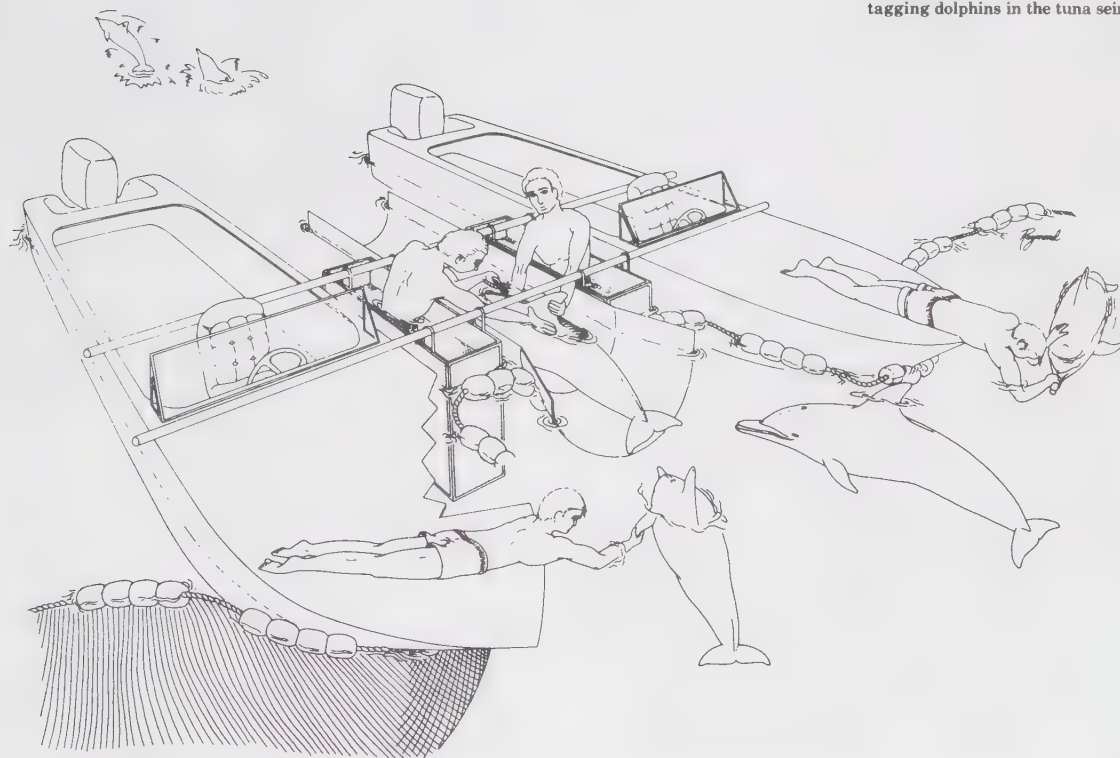


Figure 3.—Chute system used for tagging dolphins in the tuna seine.



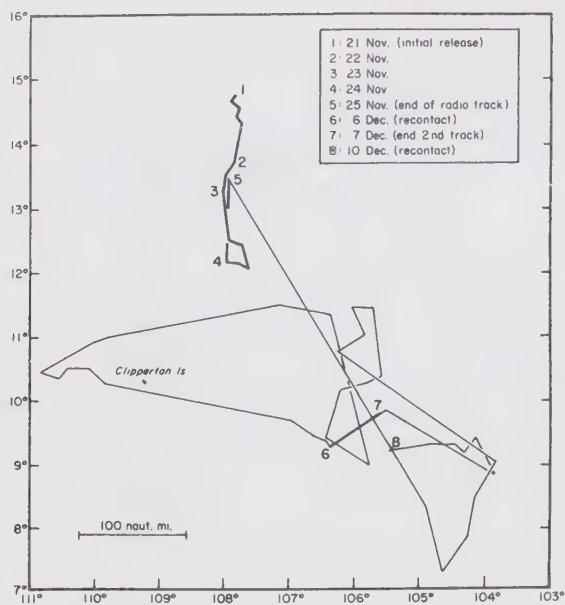


Figure 4.—Cruise track of chartered purse seiner *Queen Mary* while tracking movement of school of radiotagged spotted dolphins, *Stenella attenuata*, in November-December 1971. Heavy lines represent portions of the cruise track when radio contact was maintained with the school. The lines represent movements of the vessel, not necessarily the exact route of the radio-tagged animals.

fore completion of the net circle. After the set, A and D were followed until 2200 when they separated. Male D was followed, with a faint signal in the background from A, until 1020 on 24 November (set 5). Net distance traveled in this 24-h period was 69 n.mi., but actual distance traveled was about 110 n.mi. (Fig. 4). At this time, A and D had reconverged, but the set was made on the portion of the school containing D. Animal D again eluded capture in the seine. A and D rejoined after the set and were followed until 0700 on 25 November when the track was terminated because of an approaching storm. Net distance traveled during this 22-h period was approximately 75 n.mi. The school had doubled back and was heading north on almost exactly the same path it had followed south 3 days before. Total net distance traveled during the 110 h of the 5-day radiotrack was only about 75 n.mi., about one-fourth of the actual distance traveled. Maximum distance between any two points on the track was about 160 n.mi.

On 6 December, 11 days and approximately 285 n.mi. distance from termination of the first track, signals from both of the males (A and D) were picked up at 1255 and followed until 0750 on 7 December when strong signals were received from A in a school of <30 spotted dolphins. The school was chased to allow close approach and a good estimate of size, but no net set was made, and the school was not further followed. Net distance traveled during this 19-h second radiotrack was about 75 n.mi. Three days later, on 10 December, at 0925, signals were again received from A and D, and, this time, also from

the female C, which had not been heard from since separating from the males on 23 November. The males and females were again segregated within the school. The school was not set on or followed after this recontact, and the research cruise ended shortly thereafter. Net distance traveled by the school between initial release and last contact (19 days) was 357 n.mi. (19 n.mi./day, south-southeast).

RESULTS AND DISCUSSION

Of 3,712 tags released from 1969 through 1976, 104 had been returned as of 1 January 1977 (Tables 3, 4). Tags were recovered only from spotted dolphins (97) and spinner dolphins (7). Time at liberty ranged from 1 h and 40 min to 1,478 days for *S. attenuata* and from 15 h and 48 min to 776 days for *S. longirostris*. Minimum distance traveled (distance between release and recovery locations) ranged from 7 to 582 n.mi. for *S. attenuata* (Fig. 5) and 12 to 275 n.mi. for *S. longirostris* (Fig. 6). Details of returns are presented in Tables 4, 5. Returns are sufficient for the spotted dolphin to allow some analyses based on these and on the results of radiotagging.

Short-Term Movements

Twenty-six tagged spotted dolphins were recaptured within 2 days (48 h) after release (Fig. 7). Longer term recoveries were not included in the analysis because of the increasing potential for bias caused by the animals doubling back on themselves (see results of radiotagging experiment above). A linear regression line fitted to the data has a slope indicating an average movement rate of about 1.2 n.mi./h (about 30 n.mi./day).

The results of the radiotagging experiment indicate daily movement rates of similar scale (Fig. 4), yielding estimates of net daily travel rate ranging from 5 to 89 n.mi. and an average of 54 n.mi./day (Table 6), as compared with the estimate of about 30 n.mi./day based on short-term tag returns. The former can be assumed to be less affected by the "doubling back" factor.

Long-Term Movements

A plot of minimum distance traveled on time at liberty for all tag returns shows maximum movement of 500 to 600 n.mi. (Fig. 8). The data may have a periodic component. Average minimum distance traveled is 100 n.mi. for 10- to 50-day returns ($n = 21$) and 274 n.mi. for 50- to 200-day returns ($n = 12$) but only 93 n.mi. for 200- to 400-day returns ($n = 15$). A major question in interpreting these results is that of recovery effort. Tags are recovered during the fishing operation. Was there significantly more fishing effort in areas <200 n.mi. from areas in which tags were released 200 to 400 days earlier than in areas more than 200 n.mi. from areas of release? In other words, could the data reflect periodic fishing effort rather than periodic movement of dolphins? In an attempt to settle this question, we examined, for each of the 50- to 200-day returns (12) and each of the 200- to

Table 4.—Tag return data for spotted dolphin, *Stenella attenuata*, 1969-76. Recovered radiotags included. Tag type codes defined in text.

		Release			Recapture			Days at liberty (or h)	Minimum distance traveled (n.mi.)	Direction		Tag type	Tag number
		Date	Cruise number	Position lat. N long. W	Date	Position lat. N long. W	net movement °T bearing						
1	1 Nov 69	1055	14°17'	98°58'	1970	—	—	60	—	—	—	PD (a)	T3154
2	2 Nov 69	1055	13°49'	99°20'	25 Feb 70	15°39'	101°09'	114	152	316	NW	PD (a)	T3160
3	4 Nov 69	1055	15°03'	101°42'	3 Mar 70	15°10'	100°41'	119	59	83	E	PD (a)	T3193
4	17 Nov 69	1055	10°28'	107°40'	3 Apr 70	7°58'	98°10'	137	582	104	ESE	PD (a)	A1171
5	18 Nov 69	1055	10°58'	107°34'	19 Nov 69	10°41'	107°08'	(24 h)	31	124	SE	PD (a)	A1181
6	18 Nov 69	1055	11°09'	107°20'	5 Mar 70	13°20'	100°15'	107	435	72	ENE	PD (a)	A1199
7	11 Sep 70	—	9°46'	140°50'	3 Dec 70	9°32'	134°15'	83	390	92	E	MD (b)	P1019
8	24 Nov 71	13	12°11'	107°57'	11 Jan 72	11°37'	105°03'	48	174	101	E	MD (c)	01666
9	7 Dec 71	13	9°49'	105°29'	12 Jan 72	10°40'	106°31'	36	67	320	NW	MD (c)	00769
10	8 Dec 71	13	10°15'	104°32'	9 Dec 72	9°16'	104°26'	(15 h)	59	174	S	MD (a)	00013
11	9 Dec 71	13	9°17'	104°48'	10 Feb 72	9°16'	98°40'	63	363	90	E	MD (a)	00096
12	9 Dec 71	13	9°17'	104°48'	10 Feb 72	9°16'	98°40'	63	363	90	E	MD (a)	00099
13	11 Dec 71	26	9°21'	105°50'	12 Jan 72	10°40'	106°13'	32	82	344	NNW	DE (b)	116
14	11 Dec 71	26	9°21'	105°50'	8 Jan 72	8°50'	104°40'	28	76	144	ESE	DE (b)	118
15	13 Jan 72	14	7°10'	102°30'	1973	—	—	—	—	—	—	MD (a)	00609
16	21 Jan 72	17	10°30'	99°50'	10 Feb 72	9°50'	97°10'	20	162	104	ESE	MD (a)	00591
17	30 Jan 72	16	6°15'	98°58'	31 Jan 72	6°07'	99°36'	(21 h)	40	252	WSW	MD (a)	00434
18	24 Feb 72	16	14°54'	99°34'	4 Mar 72	14°40'	100°55'	9	80	260	W	MD (a)	00457
19	25 Feb 72	21	9°45'	98°35'	28 Mar 72	10°35'	100°55'	32	147	290	WNW	MD (a)	00475
20	27 Mar 72	22	9°28'	98°21'	11 Apr 72	13°16'	96°22'	15	256	27	NNE	MD (a)	00111
21	8 Aug 72	26	12°30'	109°23'	21 Feb 74	12°55'	99°41'	501	568	86	E	DE (b)	011
22	23 Oct 72	26	10°28'	104°03'	15 Nov 76	—	—	1478	—	—	—	DE	—
23	27 Mar 73	45	9°53'	96°17'	—	—	—	—	—	—	—	MD (a)	01425
24	6 Feb 74	61	17°37'	112°41'	3 Aug 74	19°20'	113°25'	179	111	338	NNW	MD (b)	02959
25	9 Feb 74	61	17°24'	102°24'	9 Feb 74	17°29'	102°19'	(2 h)	7	44	NE	MD (b)	02986
26	18 Feb 74	59	11°05'	90°38'	29 Jan 75	12°45'	91°43'	345	119	328	NNW	MD (a)	01457
27	18 Feb 74	59	9°37'	91°26'	6 Mar 74	11°20'	91°23'	16	103	2	N	MD (a)	01461
28	18 Feb 74	59	9°37'	91°26'	6 Mar 74	11°40'	91°50'	16	125	349	N	MD (a)	01469
29	20 Feb 74	58	14°46'	102°09'	20 Feb 74	14°39'	102°11'	(2 h)	7	188	S	MD (a)	00837
30	25 Feb 74	66	14°15'	102°20'	27 Feb 74	14°38'	102°38'	(54 h)	32	328	NNW	MD (a)	00073
31	4 Apr 74	82	5°10'	89°10'	4 Mar 75	4°22'	87°02'	334	136	111	ENE	MD (a)	00059
32	19 Jun 74	91	18°16'	115°51'	7 Mar 75	16°32'	113°30'	260	170	127	SE	MD (b)	02101
33	20 Jun 74	91	18°00'	114°50'	30 Jun 74	18°09'	115°49'	10	57	279	W	MD (b)	02699
34	21 Jun 74	91	17°54'	114°02'	22 Jun 74	17°57'	113°38'	(14 h)	23	82	E	MD (b)	02085
35	21 Jun 74	91	17°20'	114°23'	30 Jun 74	18°09'	115°17'	9	71	314	NW	MD (b)	02691
36	21 Jun 74	91	17°20'	114°23'	1 Jul 74	18°19'	114°23'	10	39	356	N	MD (b)	02694
37	22 Jun 74	91	18°27'	113°19'	13 Dec 74	20°07'	112°15'	174	117	31	NNE	MD (b)	02032
38	22 Jun 74	91	18°27'	113°19'	20 Apr 75	17°23'	114°09'	302	80	217	SW	MD (b)	02037
39	22 Jun 74	91	18°20'	113°17'	1 Jul 74	18°19'	114°23'	9	63	269	W	MD (b)	02042
40	22 Jun 74	91	18°20'	113°17'	—	—	—	—	—	—	—	MD (b)	02047
41	22 Jun 74	91	17°57'	113°38'	25 Jun 74	17°10'	115°00'	3	91	239	WSW	MD (b)	02071
42	23 Jun 74	91	18°00'	113°00'	24 Jun 74	17°53'	113°06'	(14 h)	9	219	SW	MD (a)	00395
43	23 Jun 74	91	18°00'	113°00'	15 Apr 75	18°17'	113°36'	296	38	297	WNW	MD (a)	00398
44	23 Jun 74	91	18°00'	113°00'	8 Aug 74	18°12'	114°45'	46	101	277	W	MD (b)	02029
45	26 Jun 74	91	17°50'	116°00'	20 Apr 75	17°23'	114°09'	298	109	104	ESE	MD (a)	00376
46	28 Jun 74	91	17°45'	115°00'	3 May 75	18°12'	114°20'	315	47	55	NE	MD (a)	00667
47	28 Jun 74	91	17°45'	115°00'	30 Jun 74	18°09'	115°49'	(45 h)	52	297	WNW	MD (a)	01037
48	28 Jun 74	91	17°45'	115°00'	29 Jun 74	17°57'	115°22'	(18 h)	24	300	WNW	MD (a)	01039
49	29 Jun 74	91	18°07'	115°08'	5 Aug 74	19°08'	116°00'	37	70	330	NNW	MD (a)	01016
50	29 Jun 74	91	17°57'	115°22'	30 Jun 74	18°09'	115°49'	(25 h)	28	295	WNW	MD (a)	01056
51	30 Jun 74	91	18°09'	115°49'	5 Aug 74	18°05'	114°10'	36	94	92	E	MD (a)	01023
52	30 Jun 74	91	18°09'	115°49'	5 Aug 74	19°08'	116°00'	36	60	350	N	MD (a)	01028
53	1 Jul 74	91	18°19'	114°23'	2 Jul 74	18°35'	114°40'	(17 h)	23	315	NW	MD (a)	01043
54	1 Jul 74	91	18°19'	114°23'	2 Jul 74	18°35'	114°40'	(17 h)	23	315	NW	MD (a)	01050
55	1 Jul 74	91	18°19'	114°23'	2 Jul 74	18°35'	114°40'	(17 h)	23	315	NW	MD (a)	01093
56	1 Jul 74	91	18°19'	114°23'	2 Jul 74	18°35'	114°40'	(17 h)	23	315	NW	MD (a)	01094
57	1 Jul 74	91	17°58'	114°36'	4 Aug 74	19°00'	114°26'	34	63	9	N	MD (a)	01077
58	1 Jul 74	91	17°58'	114°36'	4 Aug 74	19°00'	114°26'	34	63	9	N	MD (a)	01084
59	1 Jul 74	91	17°58'	114°36'	7 Jul 74	16°50'	114°15'	6	71	164	SSE	MD (a)	01079
60	2 Jul 74	91	18°35'	114°40'	5 Jul 74	18°18'	114°12'	3	32	123	ESE	MD (a)	01069
61	2 Jul 74	91	18°12'	114°26'	4 Aug 74	19°00'	114°23'	33	48	3	N	MD (b)	02013
62	2 Jul 74	91	18°12'	114°23'	3 Aug 74	19°20'	113°25'	32	87	39	NE	MD (b)	02018
63	5 Jul 74	91	18°23'	114°46'	9 May 75	18°12'	114°20'	308	27	114	ESE	MD (b)	02060
64	5 Jul 74	91	18°18'	114°12'	20 Apr 75	17°23'	114°09'	289	55	117	S	MD (b)	02117
65	5 Jul 74	91	18°18'	114°12'	3 Aug 74	19°20'	113°25'	29	76	36	NE	MD (b)	02118
66	31 Jul 74	91	18°28'	111°00'	16 Nov 74	20°05'	109°39'	108	124	38	NE	MD (b)	02534
67	1 Aug 74	91	19°40'	110°12'	24 Mar 75	16°00'	109°40'	235	222	172	S	MD (b)	02745

Table 4.—Continued.

		Release			Recapture			Days at liberty (or h)	Minimum distance traveled (n.mi.)	Direction		Tag type	Tag number
		Date	Cruise number	Position lat. N long. W	Date	lat. N	long. W			net movement °T bearing			
68	3 Aug 74	91	19°20'	113°25'	20 Apr 75	17°23'	114°09'	259	124	200	SSW	MD (b)	02618
69	4 Aug 74	91	19°00'	114°26'	14 Apr 75	17°07'	113°33'	252	123	156	SSE	MD (b)	02622
70	4 Aug 74	91	19°00'	114°26'	20 Apr 75	17°23'	114°09'	258	98	171	S	MD (b)	02646
71	8 Aug 74	91	18°12'	114°45'	22 May 75	17°20'	114°55'	287	53	190	S	MD (b)	02152
72	9 Aug 74	91	18°40'	113°55'	10 Apr 75	17°10'	114°15'	244	92	192	SSW	MD (b)	02155
73	17 Aug 74	91	11°15'	109°05'	18 Aug 75	11°34'	108°16'	(19 h)	52	68	ENE	MD (b)	02275
74	17 Aug 74	91	10°54'	109°13'	18 Aug 75	11°34'	108°16'	(25 h)	71	52	NE	MD (b)	02784
75	17 Aug 74	91	10°54'	109°13'	17 Aug 75	11°15'	109°05'	(5 h)	22	20	NNE	MD (b)	02786
76	17 Aug 74	91	10°54'	109°13'	17 Aug 75	11°15'	109°05'	(5 h)	22	20	NNE	MD (b)	02792
77	17 Aug 74	91	10°54'	109°13'	17 Aug 75	11°15'	109°05'	(5 h)	22	20	NNE	MD (b)	02799
78	7 Jan 75	99	20°14'	110°32'	13 Jan 75	19°35'	110°20'	6	41	164	SSE	MD (a)	01321
79	21 Jan 75	100	13°35'	100°35'	30 Mar 75	12°59'	103°00'	68	146	256	WSW	MD (d)	04509
80	30 Jan 75	102	14°47'	99°09'	3 May 75	15°31'	109°00'	93	572	276	W	MD (d)	04227
81	31 Jan 75	112	13°08'	91°50'	1 Feb 75	13°12'	91°38'	(16 h)	12	71	ENE	MD (d)	04366
82	31 Jan 75	112	13°08'	91°50'	1 Feb 75	13°12'	91°38'	(16 h)	12	71	ENE	MD (d)	04391
83	31 Jan 75	112	13°08'	91°50'	18 Feb 75	12°23'	91°38'	18	47	165	SSE	MD (d)	04377
84	18 Feb 75	112	9°25'	95°15'	5 Aug 75	9°13'	99°18'	168	240	267	W	MD (d)	04389
85	19 Feb 75	113	9°20'	95°43'	21 Feb 75	9°08'	96°55'	2	72	261	W	MD (d)	04407
86	21 Feb 75	113	9°01'	97°57'	23 Feb 75	8°32'	98°28'	2	42	227	SW	MD (d)	04413
87	21 Feb 75	113	9°01'	97°57'	23 Feb 75	8°32'	98°28'	2	42	227	SW	MD (d)	04414
88	22 Feb 75	119	12°10'	92°10'	2 Mar 75	12°48'	92°37'	8	46	325	NW	MD (d)	04963
89	14 Apr 75	121	17°07'	113°33'	21 Apr 75	17°29'	114°11'	7	42	301	NNW	MD (d)	04264
90	14 Apr 75	121	17°07'	113°33'	21 Apr 75	17°29'	114°11'	14	54	152	WNW	MD (d)	04266
91	21 Apr 75	105	14°48'	109°15'	5 May 75	14°00'	108°49'	14	54	152	SSE	MD (d)	04467
92	21 Apr 75	105	14°48'	109°15'	5 May 75	14°00'	108°49'	14	54	152	SSE	MD (d)	04468
93	24 Oct 76	208	9°33'	104°46'	26 Oct 76	9°11'	105°01'	(15 h)	26	214	SW	MD ¹	05194
94	25 Oct 76	208	9°33'	104°46'	26 Oct 76	9°11'	105°01'	(15 h)	26	214	SW	MD ¹	05200
95	25 Oct 76	208	9°33'	104°46'	26 Oct 76	9°11'	105°01'	(15 h)	26	214	SW	MD ¹	05217
96	25 Oct 76	208	9°33'	104°46'	26 Oct 76	9°11'	105°01'	(15 h)	26	214	SW	RX	—
97	25 Oct 76	208	9°33'	104°46'	26 Oct 76	9°11'	105°01'	(15 h)	26	214	SW	RX	—

¹With braided tubing.Table 5.—Tag return data for spinner dolphin, *Stenella longirostris*, 1969-76. Tag type codes defined in text.

		Release			Recapture			Days at liberty (or h)	Minimum distance traveled (n.mi.)	Direction of		Tag type	Tag number
		Cruise number	Position		Date	Position				net movement °T bearing			
			lat. N	long. W		lat. N	long. W						
1	18 Aug 70	26	10°47'	127°48'	17 Sep 71	11°17'	123°09'	395	275	83	E	PD (a)	A6242
2	23 Nov 71	13	13°20'	108°00'	8 Jan 74	11°44'	105°32'	776	172	124	SE	MD (a)	01116
3	8 Dec 71	13	10°15'	104°32'	28 Feb 72	11°01'	101°15'	82	199	76	ENE	MD (a)	00741
4	8 Dec 71	13	10°15'	104°32'	28 Feb 72	11°01'	101°15'	82	199	76	ENE	MD (a)	00016
5	10 Jan 72	16	9°04'	105°01'	6 Feb 72	9°35'	108°10'	37	189	280	W	MD (a)	00413
6	31 Jan 75	112	13°08'	91°50'	1 Feb 75	13°12'	91°38'	(16 h)	12	71	ENE	MD (d)	04363
7	13 Apr 75	105	6°38'	93°21'	16 Apr 75	6°54'	94°43'	3	83	281	W	MD (d)	04464

Table 6.—Net distance traveled and net travel rates for radiotrack segments <50 h long.

Track segment (Fig. 4)	Duration (h)	Minimum distance (n.mi.)	N.mi. h	N.mi. day
1-2 (set)	16	59	3.7	89
2-3 (set)	24	28	1.2	29
3-4 (set)	24	69	2.9	70
4-5	22	75	3.4	82
1-3 (set)	40	70	1.8	43
2-4 (set)	48	80	1.7	41
3-5	46	10	0.2	5
6-7 (chase)	19	60	3.2	77
Average	—	—	2.3	54

400-day returns (15), the logged take of yellowfin tuna⁵ within a radius of 250 n.mi. and a radius of 250 to 600 n.mi. during the period after 50 days following release and before capture, or after 200 days and before recapture, respectively (Table 7) (catch of yellowfin tuna is the closest correlate of actual tag recapture effort (i.e., number of dolphins captured) for which data of sufficient geographical and temporal precision are available). For both groups of tag returns, the catch of yellowfin tuna in each instance was greater in the 250- to 600-

⁵Unpublished data furnished by J. Joseph, Inter-American Tropical Tuna Commission, P.O. Box 271, La Jolla, CA 92038.

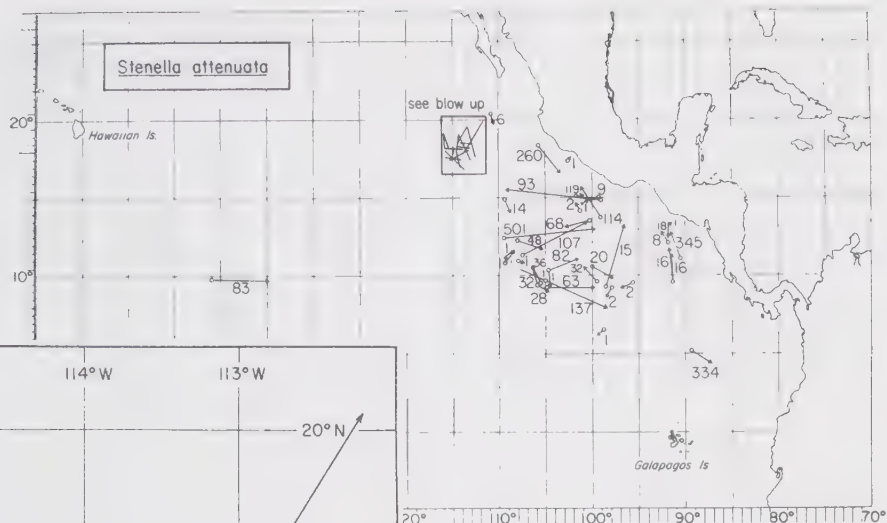


Figure 5.—(Top) Minimum distance and net direction of travel, with days at liberty, of spotted dolphins, *Stenella attenuata*, tagged 1969-76 and recaptured before 1 January 1977. Returns from radio transmitters not included. (Bottom) Blow up of inset.

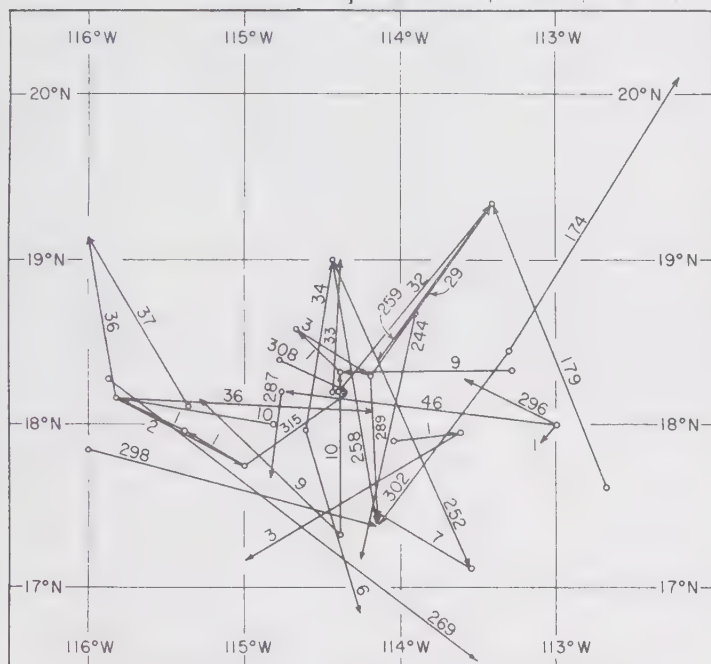
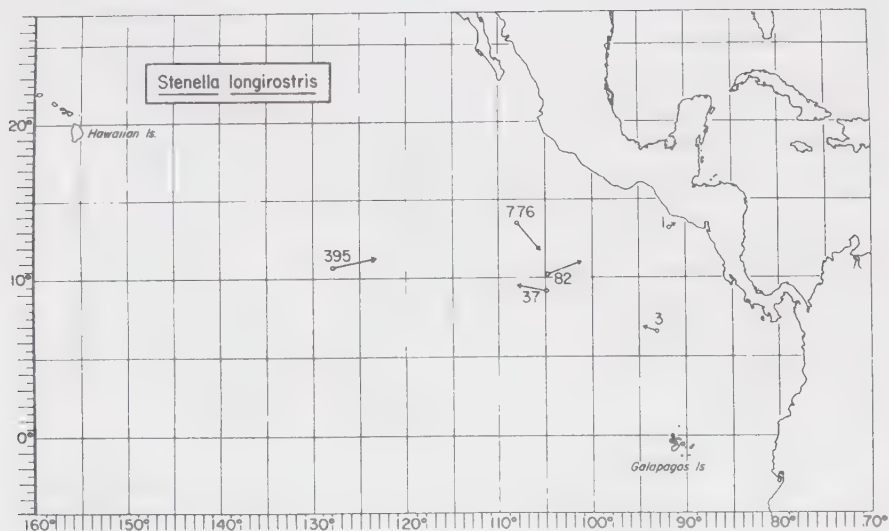


Figure 6.—Minimum distance and net direction of travel, with days at liberty, of spinner dolphins, *Stenella longirostris*, tagged 1969-76 and recaptured before 1 January 1977.



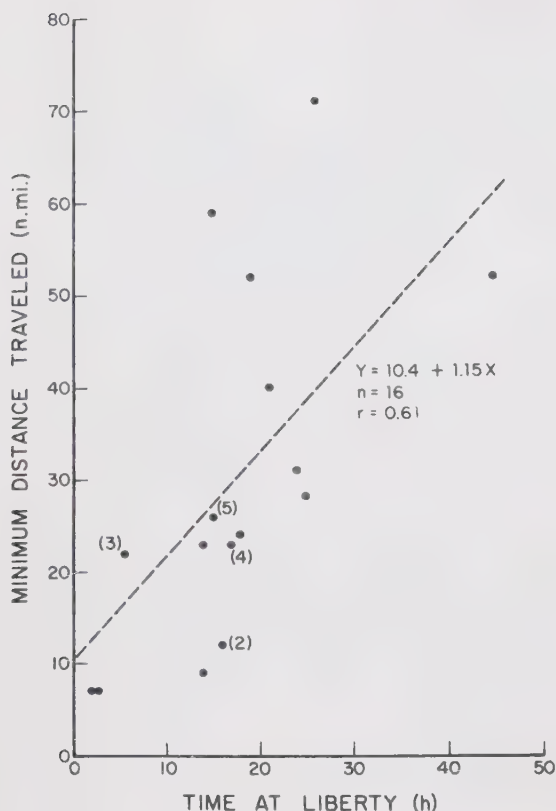


Figure 7.—Movement of tagged spotted dolphins, *Stenella attenuata*, recaptured within 48 h of release. When more than one dolphin was tagged and recovered from the same school at the same time, the number is indicated in parentheses. Dashed line is linear regression line fitted to unweighted data points.

n.mi. area than in the 250-n.mi. area. This result shows that the pattern in Figure 8 of apparent annual migration or dispersal of at least some of the tagged animals is real and not an artifact of the distribution of recapture effort.

The net direction of movements of <300 n.mi. was essentially random, but movements >300 n.mi. had a very strong east-west component (Fig. 9). This apparent predominance of longitudinal movement in long-distance returns is probably not due to chance. If it is assumed that the distribution of deviations in Figure 8 would be random, given that neither longitudinal nor latitudinal movement predominate, the probability that all seven of the over 300 n.mi. net movements would have deviations of <20° is described by a binomial probability distribution. If $n = 7$ and $P = 90$, then the probability is 2.6×10^{-5} . The data, therefore, show that, if seasonal migration or dispersal does indeed exist, it is primarily onshore-offshore. The time-of-year data for the few tag returns indicating movements >300 n.mi. indicate that movement may be generally onshore (E) in fall and winter and offshore (W) in late spring and summer

Table 7.—Estimated catch of yellowfin tuna within 250 n.mi. and within 250-600 n.mi. of point of tag release for 12 tagged dolphins recovered between 50 and 200 days after release and traveling up to 582 mi (average 174 mi) and 15 tagged dolphins recovered between 200 and 400 days after release and traveling <223 mi (average 93 mi). Catches for the first group are between 50 days after release and before recapture and for the second group between 200 days and recapture.

Tag returns	Estimated yellowfin tuna catch	
	Within 250 n.mi. (short tons)	Within 250-600 n.mi. (short tons)
Group 1		
(50-200 days):		
1.	886	14,041
2.	9,363	25,908
3.	4,858	35,508
4.	4,728	30,119
5.	76	657
6.	2,065	11,906
7.	2,365	4,562
8.	745	1,529
9.	516	1,501
10.	1,202	7,885
11.	1,436	4,497
12.	4,737	6,605
Group 2		
(200-400 days):		
1.	5,108	6,224
2.	2,396	26,142
3.	470	6,325
4.	4,656	14,737
5.	4,523	16,180
6.	3,277	12,389
7.	3,893	14,452
8.	3,893	13,126
9.	4,485	13,573
10.	1,955	3,177
11.	3,051	6,746
12.	952	3,611
13.	3,214	6,377
14.	5,390	13,312
15.	759	3,944

Table 8.—Time of year at liberty and net direction of movement for seven tagged spotted dolphins, *Stenella attenuata*, traveling more than 300 n.mi. before recapture.

At liberty	Net movement	
	Direction	Distance (n.mi.)
1. Jan-May	W	572
2. Aug-Feb	E	568
3. Sept	E	390
4. Nov-Mar	ENE	435
5. Nov-Apr	ESE	582
6. ¹ Dec-Feb	E	363

¹Two dolphins.

(Table 8). This hypothesis must be considered as highly tentative, however, pending availability of more data.

In summary, home range at any particular season is roughly circular, on the order of 200 to 300 n.mi. in diameter, and may move seasonally several hundred miles onshore (possibly in fall and winter) and offshore (possibly in spring and summer). Average short-term net movement is on the order of 30 to 50 n.mi./day.

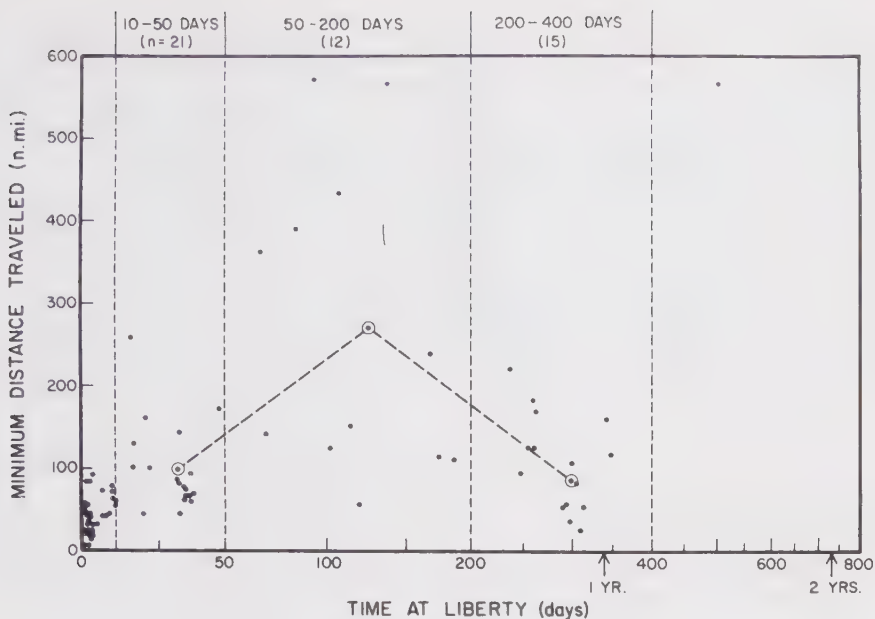


Figure 8.—Plot of minimum distance traveled on time at liberty (logarithmic scale) for tagged and recaptured spotted dolphins, *Stenella attenuata*. Circled means are for 10- to 50-, 50- to 200-, and 200- to 400- day returns.

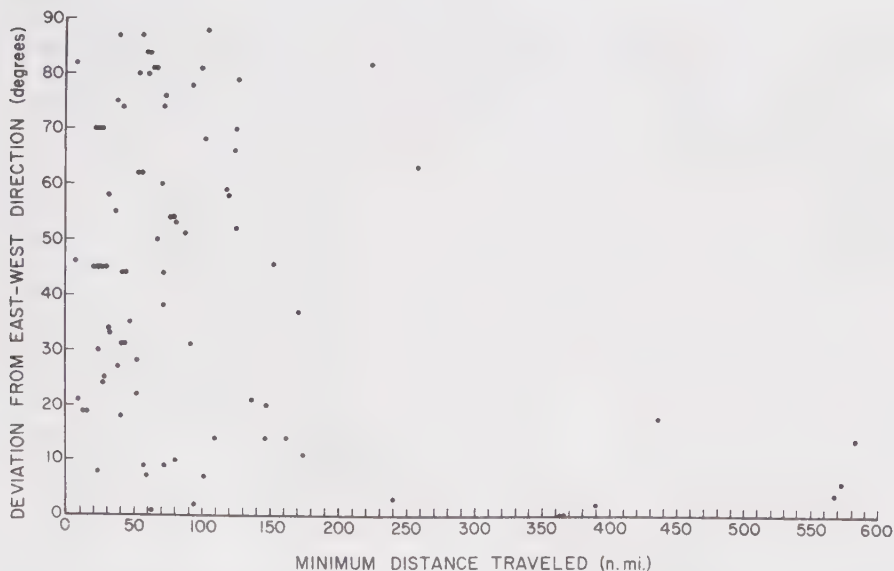


Figure 9.—Deviation from E-W direction of net movement plotted on minimum distance traveled for tagged and recaptured spotted dolphins, *Stenella attenuata*.

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We thank the hundreds of people (scientists, technicians, crew members, and vessel owners and operators) who helped get the tags out and the recoveries in. Some are mentioned in the text; others (including the many "tunaboat observers" who released the tags listed in Appendix 2) are not. We thank W. H. Bayliff who proposed the initial design of the tagging shute. We also thank J. G. Jennings, J. M. Coe, T. Quinn, V. I. Gallucci, R. L. Brownell, Jr., and W. H. Bayliff, for criticizing the manuscript. Unpublished data were furnished by the Inter-American Tropical Tuna Commission through the courtesy of C. J. Orange. R. Butler and N. K. Wiley provided invaluable assistance with data processing.

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Taxonomic Status of the 'Southwestern Stocks' of Spinner Dolphin *Stenella longirostris* and Spotted Dolphin *S. attenuata*

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ABSTRACT

Spinner dolphins, *Stenella longirostris*, and spotted dolphins, *S. attenuata*, from south of the equator in the eastern Pacific are modally different from dolphins of the same species just to the north in coloration, size, shape and skeleton. These populations, called here "southern spinner dolphin" and "southern spotted dolphin" are potential management entities.

At the time a workshop meeting to assess stocks of dolphins involved in the seine fishery for tropical tuna in the eastern tropical Pacific convened at La Jolla in August 1976 (SWFC, 1976), sketchy information was available for both the spinner dolphin, *S. longirostris*, and the spotted dolphin, *S. attenuata*, suggesting that animals observed south of the equator and west of the Galapagos Islands are morphologically different from those to the north and east. Pending further study, these tentatively identified "Southwestern stocks" were provisionally lumped with the offshore stocks of the respective species for assessment. The purpose of this report is to present the results of study of series of "Southwestern" spotted and spinner dolphins, with recommendations for partition of management units in the two species in the eastern Pacific.

SPINNER DOLPHIN

Several geographical forms of the spinner dolphin exist in the eastern tropical Pacific (Perrin, 1975a, 1975b). These include the "eastern spinner", occurring near the coast of Mexico, south to at least the equator and offshore several hundred miles. The range of the eastern spinner broadly overlaps that of the more offshore "whitebelly spinner", which extends west to about 145° W longitude. The "Costa Rican spinner" occurs only along the Pacific coast of Central America, and the "Hawaiian spinner" occurs close to shore around the Hawaiian Islands. These geographical forms were defined on the basis of shape, size, coloration and skeleton (Perrin, 1975a, 1975b) and have been considered to be more or less independent "stocks" for purposes of assessment and management (SWFC, 1976).

The first indication of existence of a morphologically distinct form of spinner dolphin south of the equator came from observations by W. E. Evans and D. W. Rice on a US-USSR cooperative whale-tagging cruise of the R/V *Vnushitel'nyi* in early 1975. They sighted several schools of spinner dolphins during the cruise (Fig. 1) and noted unusual coloration in animals seen south of the Galapagos. Both observers have had extensive prior field experience with spinner dolphins north of the equator. Following is an excerpt from Rice's field journal describing animals seen at about 4° S latitude, 99° W longitude on 13 March 1975:

"These animals resembled Hawaiian spinner porpoises in their three-tone color pattern, but had shorter beaks. The lateral gray area was somewhat darker immediately adjacent to the sharply defined white belly, giving the appearance of a faint lateral stripe. The dorsal fins were high and triangular — even slightly canted forward on

some of the larger ones. The animals appeared to have dark-tipped snouts and eye-to-flipper stripes."

Field sketches by both Evans and Rice and a photograph by Evans all show the ill-defined lateral stripe described by Rice and not seen by these or other observers as part of the color pattern of "whitebelly spinners" to the north.

Unusually marked spinner dolphins were seen again in February 1976 by W. A. Walker (also experienced in identifying spinner dolphins) during a survey cruise of the R/V *David Starr Jordan* (Fig. 2), at three locations south of the Galapagos. Following is an excerpt from his sighting notes for 15 February 1976:

"These animals more closely resemble Hawaiian stock than those in vicinity of Clipperton [Island]. Lateral overlay of cape gives an almost stripe like effect running from eye to vent, . . .".

"The border of the cape and lateral white field was distinct on these porpoise. No mottling was evident."

The summary report for the cruise¹ stated concerning the seven sightings of spinner dolphins during the cruise:

"Four of the seven schools were classified as whitebelly spinners. All of these observations were slightly outside the historically understood boundaries. However, the three observations made at about 05°–06° S appear, from color pattern differences, to be a separate stock from those normally encountered in the far offshore waters from approximately 800 km offshore to 140° W longitude."

The observations from the cruises of the R/V *Vnushitel'nyi* and the R/V *David Starr Jordan* constituted the information available to the stock assessment workshop at La Jolla in August 1976 and were the basis for provisionally considering a "tentatively identified southwestern stock" (NMFS, 1977). Specimens collected south of the equator subsequently became available and have allowed further evaluation of the "southwestern stock".

MATERIALS AND METHODS

Treatment of Specimens

Fifteen frozen carcasses of *S. longirostris* from south of the equator and west of 90° W longitude were available for study (Table 1). They were collected by NMFS observers during

¹ Barham, E. 1969. Cruise Report, R/V *David Starr Jordan*, Cruise J-76-1(100), Porpoise Cruise No. 169. Unpubl. Rep., Southwest Fisheries Center, La Jolla, Calif. 92038.

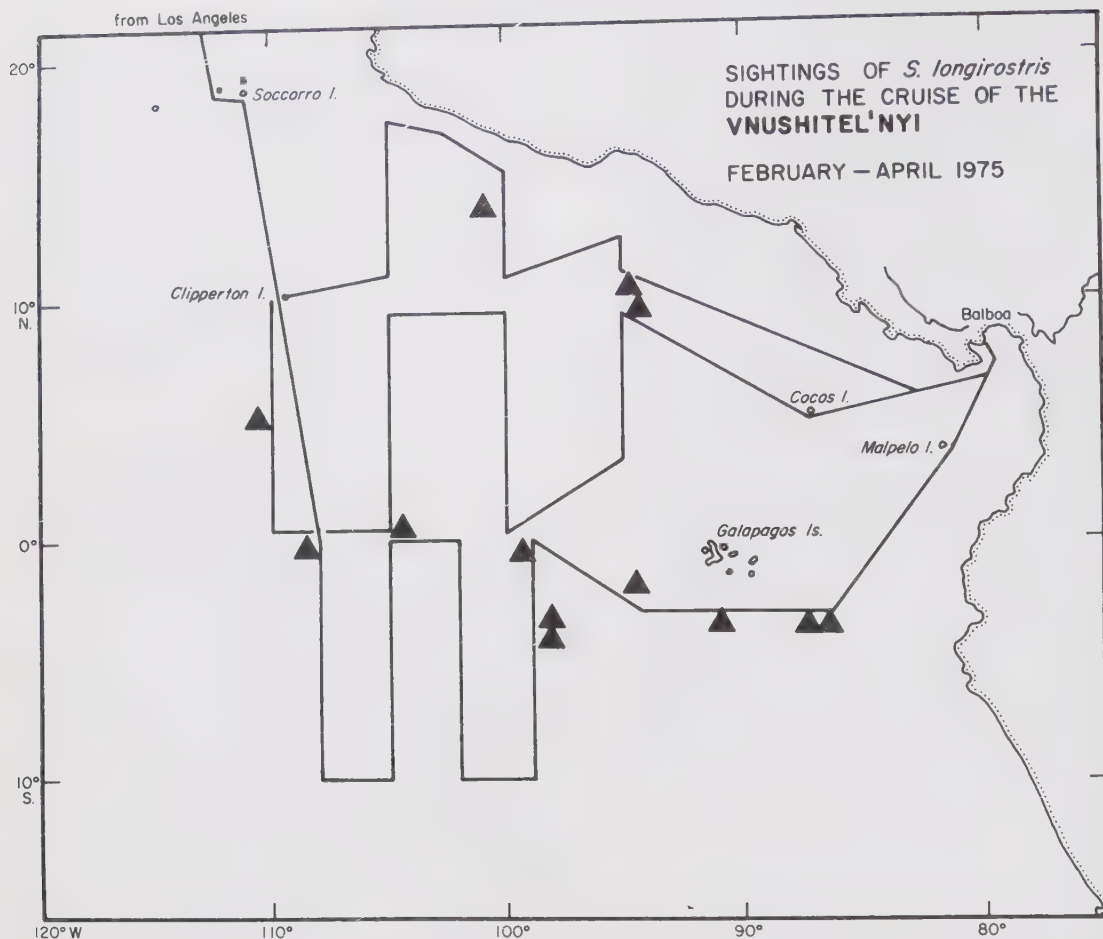


Fig. 1. Sightings of *Stenella longirostris* during the cruise of the *Vnushitel'nyi*, February to April 1975.

seining operations in early 1976. The specimens were thawed in water, weighed to the nearest pound on a platform balance, and photographed in color. External measurements were taken with a large set of calipers with adjustable jaws. Lengthwise measurements were taken parallel to the long axis of the body. Enough flesh was then removed from the carcass to allow vertebral counts to be made. The terminal 20–30 cm of the vertebral column was severed and x-rayed to determine the number of vertebrae. The flippers were also detached and x-rayed for phalangeal counts. The skulls were fleshed, sun-dried, and cleaned with dermestid beetles. Skull measurements were taken as described by Perrin (1975a). After measurement, the skulls were placed in the marine mammal collection of the Museum of Comparative Zoology, Harvard University, Cambridge, Mass. The postcranial skeletons were not saved.

In addition to the extensive data from the 15 whole specimens, a lesser set of data was available for 118 adult specimens (61 males and 57 females) examined at sea by government scientists aboard commercial tuna seiners in the area south of the equator and west of 90° W longitude (Fig. 3). These data included total length, reproductive condition (weight of testes for males; uterine, ovarian and lactation data for females), and, in some cases, field sketches and photographs.

RESULTS

Color Pattern

The modal color pattern (Fig. 4) indeed more resembles that of spinner dolphins from around Hawaii than that of the whitebelly spinner dolphin as described from north of the equator (Perrin, 1973, 1975a, 1975b), in two respects:

- (1) The dorsal overlay is sufficiently light that the dorsal cape shows through distinctly, yielding a pronounced tripartite pattern, as opposed to a basically two-part pattern in the northern whitebelly form yielded by a more dense dorsal overlay; and
- (2) the ventral margin of the dorsal overlay is relatively sharp and smooth, as compared to a usually more diffuse margin in the typical whitebelly spinner, again emphasizing the three-part character of the pattern.

The reported lateral stripe turns out not to be an actual stripe, but an increase in density of the dorsal overlay toward its ventral margin. On close inspection the animal does not have a well-defined stripe, but in the water it appears striped. Again, the appearance is quite like that of many Hawaiian spinners in this respect (Fig. 5).

The color pattern differences between this animal and the whitebelly spinner to the north are modal differences

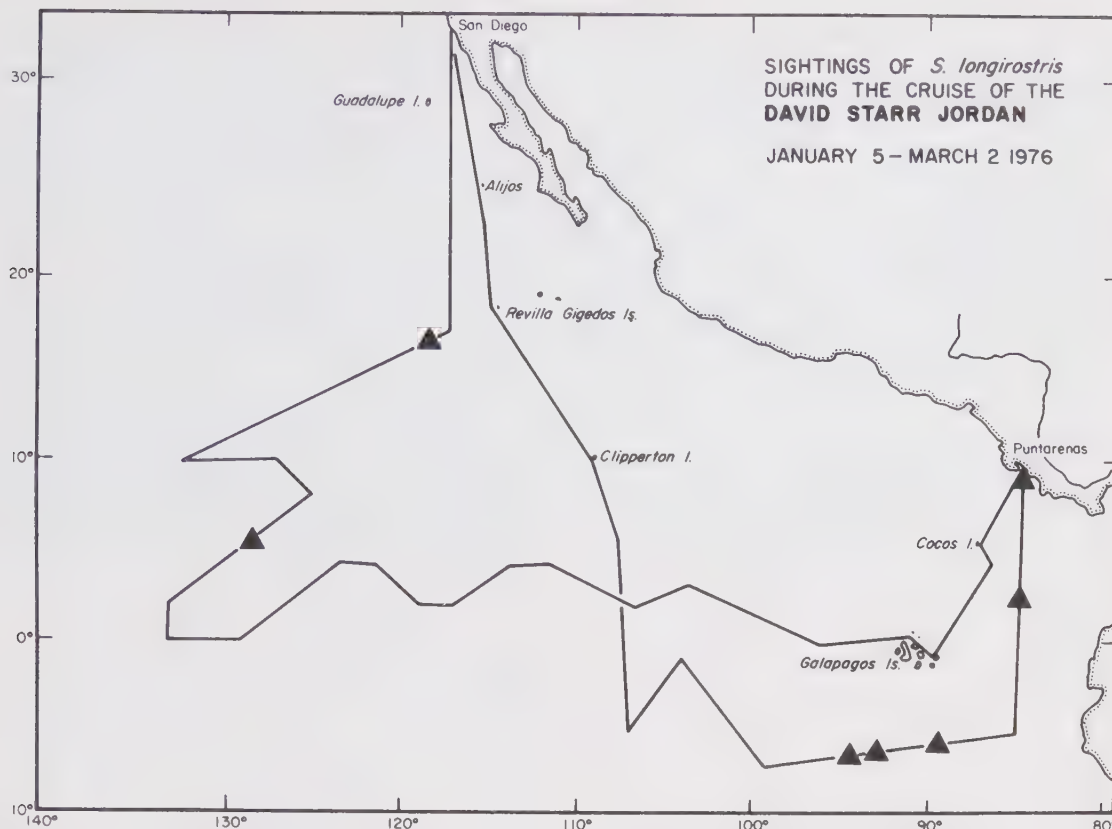


Fig. 2. Sightings of *Stenella longirostris* during cruise of David Starr Jordan, 5 January to 2 March 1976.

and do not occur with the same density for every animal in the population. As is the case for populations where morphological characters vary in this manner geographically, some individuals from either of the adjacent areas (north or south of the equator) most resemble typical animals from the other area. For example, some of the 15 individuals examined here (specimen numbered DBF 026 in Fig. 4, for example) had a more dense dorsal overlay with a less-emphasized ventral margin than the others and appeared more "whitebelly-like".

External Size and Shape

Both males and females (Fig. 6) are on the average 2–3 cm longer than whitebelly spinners (Table 2 and Fig. 13 in Perrin, Holts and Miller, 1976), a statistically significant difference ($\alpha = 0.05$). The sample sizes for other external measurements (Table 2) are small, but the means for the "southwestern" series are greater than those for a similarly sized series of whitebelly spinners (Table 16 in Perrin, 1975a) for all the measurements except "tip of snout to blowhole", for which the means are the same. For the two external measurements which most reflect length of the beak, that is, "tip of snout to apex of melon" and "length of gape", the ranges for the series fall below the ranges for the small series of Hawaiian spinners, but for the remaining measurements the ranges overlap considerably, suggesting that while the "southwestern spinner", like the Hawaiian spinner, is on the average larger than the whitebelly spinner,

its beak is not proportionately as long as that of the Hawaiian spinner, a finding consonant with the above-cited field observations.

The dorsal fin (Fig. 7) is shaped differently in males and females but is highly variable and not apparently different from that of the whitebelly spinner (Perrin, 1975a).

Skeleton

The means for nearly all the skull measurements (Table 3) fall between the means for whitebelly and Hawaiian spinners (Table 19 in Perrin, 1975). The exceptions are "premaxillary width at rostrum midlength" and "internal nares width", for which the "southwestern" means exceed the Hawaiian means. The "southwestern" skulls fall between the whitebelly series and Hawaiian series in shape as well as size, as shown by a scatterplot (Fig. 8) on two orthogonal discriminant axes based on all 25 measurements for Costa Rican, eastern, and whitebelly series (loading coefficients in Perrin, 1975).

SPOTTED DOLPHIN

As in the spinner dolphin, several geographical forms of the spotted dolphin, *Stenella attenuata*, exist in the eastern tropical Pacific (Perrin, 1975a, 1975b). A "coastal" form (formerly known as *S. graffmani*) is found close to shore from the Gulf of California to Colombia. Offshore and

Table 1

Collection data for whole frozen specimens of *S. longirostris* from south of the equator and west of 90° W longitude. Museum of Comparative Zoology (MCZ) number in parentheses

Specimen no.	Locality (lat./long.)	Date	Sex	Length (cm)
1. DBF 010 (57240)	4° 00' S/94° 25' W	30 Oct. 76	F	180
2. DBF 011 (57241)	"	"	M	170
3. DBF 012 (57242)	"	"	F	177
4. DBF 013 (57243)	"	"	M	183
5. DBF 017 (57244)	5° 05' S/94° 26' W	31 Oct. 76	M	183
6. DBF 020 (57245)	"	"	M	182
7. DBF 024 (57246)	"	"	F	170
8. DBF 026 (57247)	"	"	M	182
9. DBF 031 (57248)	"	"	F	187
10. DBF 035 (57249)	"	"	M	181
11. DBF 036 (57250)	"	"	M	188
12. DBF 038 (57251)	5° 25' S/92° 33' W	4 Nov. 76	M	186
13. DBF 040 (57252)	"	"	F	175
14. DBF 042 (57253)	3° 41' S/92° 36' W	6 Nov. 76	F	187
15. DBF 043 (57254)	"	"	F	177

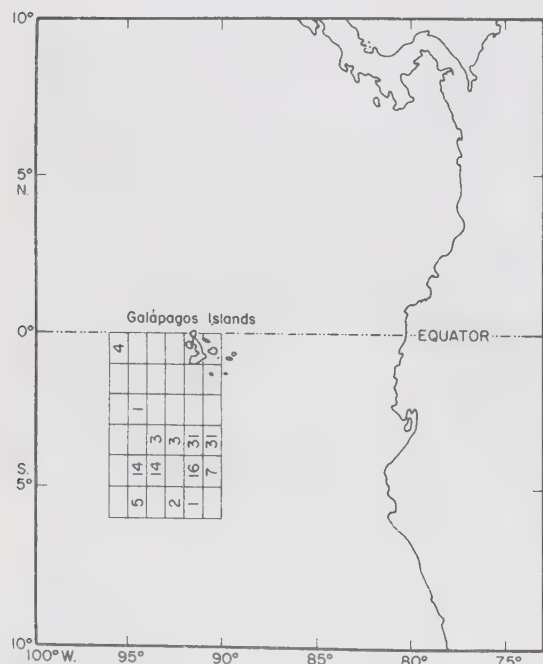


Fig. 3. Collection localities of 132 adult specimens of *Stenella longirostris* used in analysis of total length, by one-degree square areas.

north of the equator, the "offshore" spotted dolphin ranges west to about 145° W longitude. As for the spinner dolphin, the first indication of the existence of an additional geographical form south of the equator came from observations made on the R/V *Vnushitel'nyi* in 1975. One school of spotted dolphins was seen south of the equator during the cruise, at 00° 52' S latitude, 98° 44' W longitude. These animals had an overall lighter color pattern, with more contrasting elements, and were more lightly spotted than typical spotted dolphins to the north. W. E. Evans' field notes for the sighting on 17 March state:

"All spotters looked like two-tone or speckled [early coloration growth phases in more northerly spotted dolphins (Perrin, 1970)] — cape very visible."

Such coloration is characteristic of spotted dolphins in the far-western regions of the range in the eastern Pacific and around Hawaii (Perrin, 1975a). Because of this seemingly parallel situation to that for the spinner dolphin, spotted dolphins south of the Galapagos were considered by the stock assessment workshop in 1976 in a provisional "south-western stock" like that erected for the spinner dolphins (SWFC, 1976).

MATERIALS AND METHODS

Nineteen whole carcasses (6 males and 13 females) were available for study, from two localities southwest of the Galapagos (Table 4). Treatment was the same as for the specimens of *S. longirostris*. Total length and color pattern data were available for 34 additional adult males and 78 adult females examined at sea aboard commercial tuna seiners (Fig. 9). Testis samples were not collected for the males examined at sea, so an approximate criterion of adulthood of 170 cm total length (see Perrin, Coe and Zweifel, 1976) was used for inclusion in the sample of "adult" animals here.

RESULTS

Color Pattern

Of the 11 specimens with "adult coloration" (defined in Perrin, 1970), 1 showed heavy dorsal spotting, 6 had medium spotting, and 4 had sparse spotting. This distribution is similar to that in spotted dolphins from the far-offshore portion of the range in the eastern Pacific (Perrin, 1975a). The animals were generally more heavily spotted, however, than animals from around Hawaii.

External Size and Shape

Spotted dolphins south of the equator are on the average about 2–1/2 cm shorter than those to the north. Not enough gonadal specimens have been collected to allow comparison of means for sexually mature adult males, but the 91 sexually mature females examined here (Fig. 10) averaged 184.8 cm, as opposed to 187.2 cm (range 165–211, SD 7.12) for 2,433 "offshore" females from north of the equator (data collected by government scientists aboard commercial tuna seiners). This difference is significant at the 0.1% level. Despite this overall lesser size, several anterior external measurements (Table 5), especially that of "tip of snout to anterior insertion of flipper" are comparable for specimens from north (Table 5 in Perrin, 1975a) and south of the equator, indicating that the southern animals have proportionately larger heads. This is supported by the skull measurements discussed below.

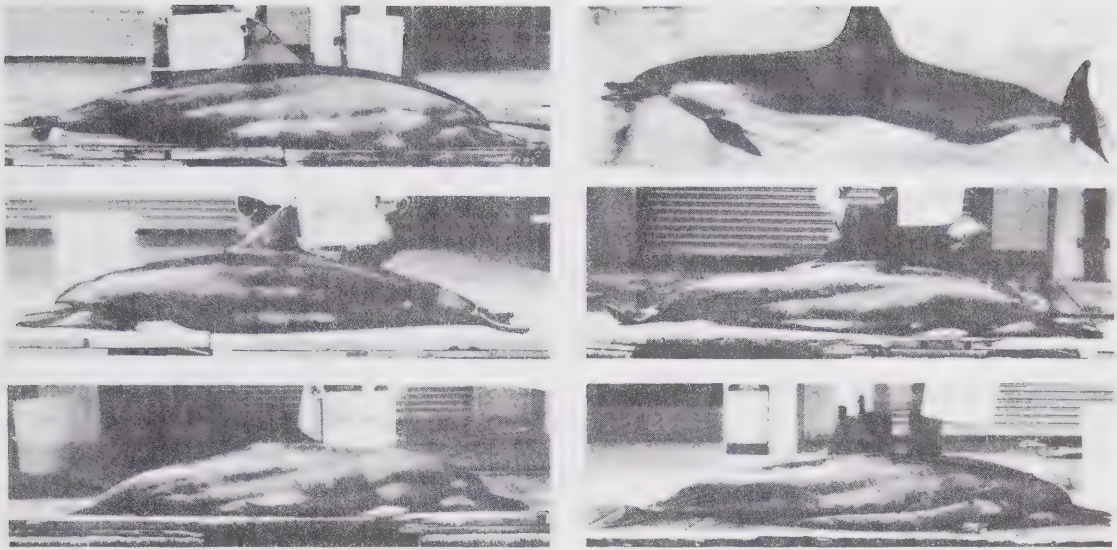


Fig. 4. External appearance (after freezing and thawing) of spinner dolphins from below the equator and west of 90° W longitude.

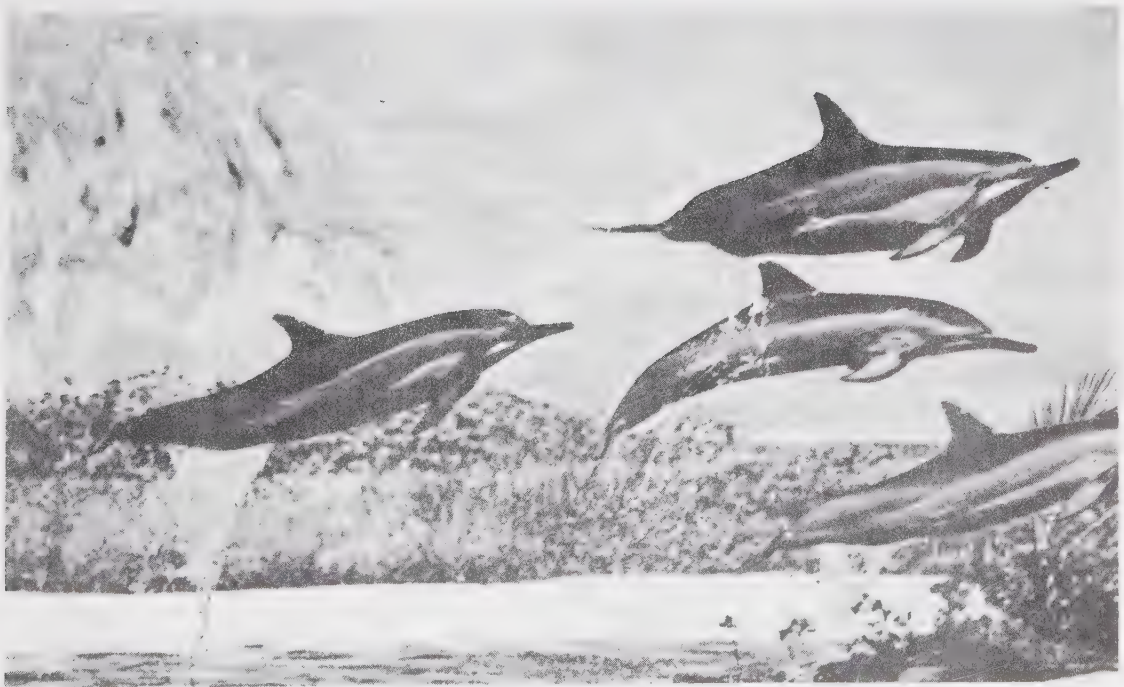


Fig. 5. Captive Hawaiian spinner dolphins.

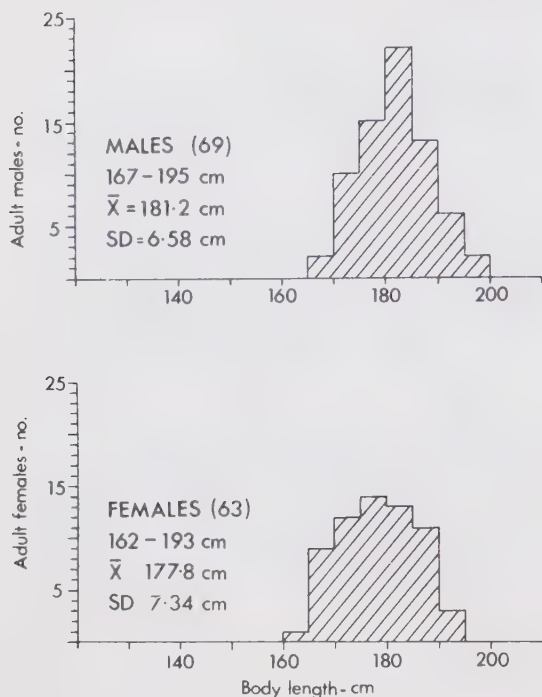


Fig. 6. Total length of adult spinner dolphins from south of the equator and west of 90° W longitude.

Skeleton

For most skull measurements, the means for the series of specimens from below the equator (Table 6) falls between those for the more northerly "offshore" spotted dolphin and the spotted dolphin around Hawaii (Tables 13a, 13b in Perrin, 1975a). The three series do not differ significantly from each other in proportions of the braincase (length, width, and height). For the single feature in which the Hawaiian spotted dolphin is smaller than "offshore" spotted dolphins, the post-temporal fossa (length and width), the "southwestern" series is comparable to the Hawaiian form.

Table 2

External measurements of sexually mature spinner dolphins, *S. longirostris*, from south of the equator and west of 90° W longitude. Measurements (in cm) follow Perrin (1975a). Males included have testis weight ≥ 94 g. Males and females pooled for dimensions in which spinner dolphin not sexually dimorphic (*ibid.*).

Measurement	Sample size	Range	Mean	Standard deviation
Total length				
(M)	7	170-186	181.0	5.03
(F)	6	175-187	180.3	5.15
Tip of snout to center eye	13	28-33	30.3	1.41
Tip of snout to apex of melon				
(M)	7	13-16	14.8	1.30
(F)	6	14-17	15.2	1.12
Length of gape	13	24-30	26.2	1.53
Tip of snout to blowhole	12	25-33	29.4	2.27
Tip of snout to anterior insertion of flipper	13	40-44	41.6	1.08
Tip of snout to tip of dorsal fin				
(M)	7	98-104	100.4	2.28
(F)	6	99-109	104.6	4.39
Tip of snout to umbilicus	13	84-95	88.8	3.81
Girth at axilla				
(M)	7	78-90	83.6	4.53
(F)	6	80-87	88.3	2.50
Flipper length to axilla	13	18-22	20.7	1.12
Fluke span				
(M)	7	37-45	41.3	3.36
(F)	6	36-41	38.5	2.07

A plot of the means for two skull indices for dolphins from three areas (coastal, offshore and Hawaiian) (Fig. 11) indicates that the skulls of the animals from south of the equator are intermediate between the far-offshore and Hawaiian forms in shape as well as size.

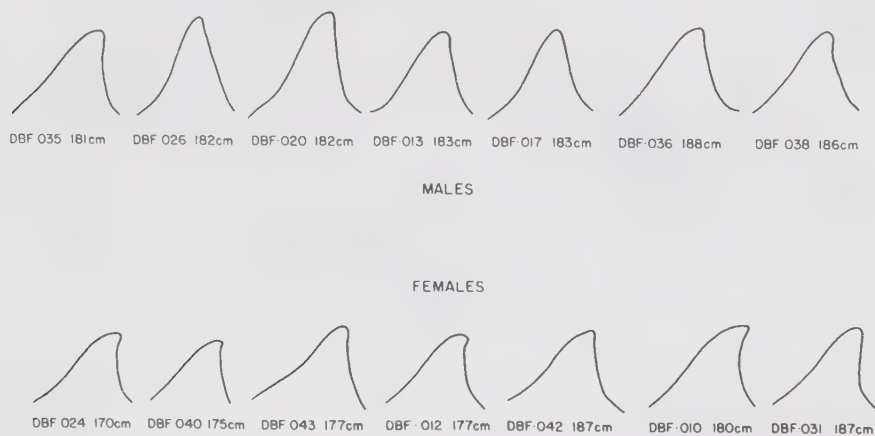


Fig. 7. Dorsal fins of male (upper) and female (lower) spinner dolphins from south of the equator and west of 90° W longitude. Specimen numbers and length (cm) given.

Table 3

Skeleton measurements (in mm) and meristics of spinner dolphins, *S. longirostris*, from south of equator and west of 90° W longitude. Numbering system follows Perrin (1975a). Sample for meristics includes all specimens, sample for measurements includes sexually mature specimens (using criterion of distal fusion of maxillaries and premaxillaries).

Variable	Sample	Range	Mean	Standard deviation
1. Condylobasal length	12	398-438	415.8	11.86
2. Rostrum length	12	250-278	265.3	10.36
3. Rostrum width at base	14	71-83	76.4	3.00
4. Rostrum width at 60 mm	14	51-60	53.4	3.56
5. Rostrum width at midlength	11	41-51	42.3	2.70
6. Premaxillary width at rostrum midlength	12	17-23	20.8	1.89
7. Rostrum width at ¼ length	12	29-36	32.0	2.17
8. Rostrum tip to external nares	12	287-318	304.3	10.19
9. Rostrum tip to internal nares	12	291-327	308.2	10.76
10. Preorbital width	14	138-150	143.6	3.81
11. Postorbital width	14	154-167	159.6	4.10
12. Least supraorbital width				
13. External nares width	14	38-46	42.1	2.24
14. Zygomatic width	14	156-165	158.1	4.36
15. Greatest width of premaxillaries	14	60-67	63.9	2.44
16. Parietal width	14	123-139	130.4	5.04
17. Braincase height	14	86-98	90.3	3.64
18. Braincase length	14	102-113	105.2	3.42
19. Posttemporal fossa length	14	41-56	49.9	4.31
20. Posttemporal fossa width	14	37-45	41.3	2.12
25. Orbit length	14	39-45	40.7	1.48
26. Internal nares width	14	44-50	46.4	1.65
32. Upper tooth row length	12	208-246	229.0	10.62
33-36. Teeth (no.) U.L. U.R.	13 13	46-59 49-59	53.1 53.5	4.05 3.50
L.L. L.R.	15 12	44-59 46-58	51.1 51.9	4.26 4.23
37. Lower tooth row length	14	193-236	221.6	11.79
38. Ramus length	14	322-374	351.4	13.34
39. Ramus height	14	51-60	55.2	2.32
48. Thoracic vertebrae (no.)	15	15-17	16.1	0.59
49. Lumbar vertebrae (no.)	15	16-18	16.5	0.63
50. Caudal vertebrae (no.)	15	32-38	34.5	1.40
51. Total vertebrae (no.)	15	72-77	74.1	1.24

CONCLUSIONS AND RECOMMENDATIONS

The "southwestern" spinner dolphins are clearly modally different from the whitebelly spinners to the north and very much like the spinner dolphins around Hawaii, albeit with proportionately smaller beaks. This morphological difference between the animals north and south of the equator leads to the inference that some degree of genetic isolation exists, i.e., that the spinner dolphins south of the equator largely belong to a different breeding population than those to the north. This conclusion speaks for consideration of separate management of the apparent two populations.

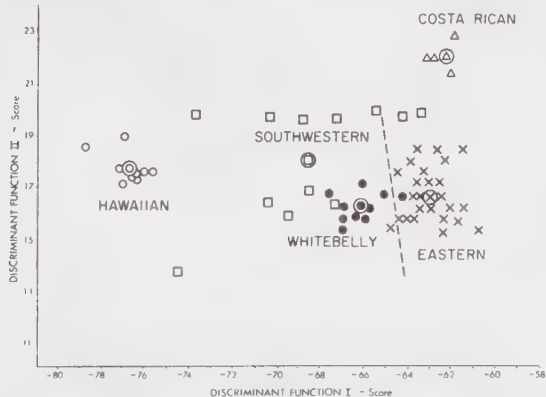


Fig. 8. Plot of "southwestern" specimens (squares) on two discriminant axes based on 25 skull measurements (discriminant functions in Perrin, 1975a). Circled symbols are group means.

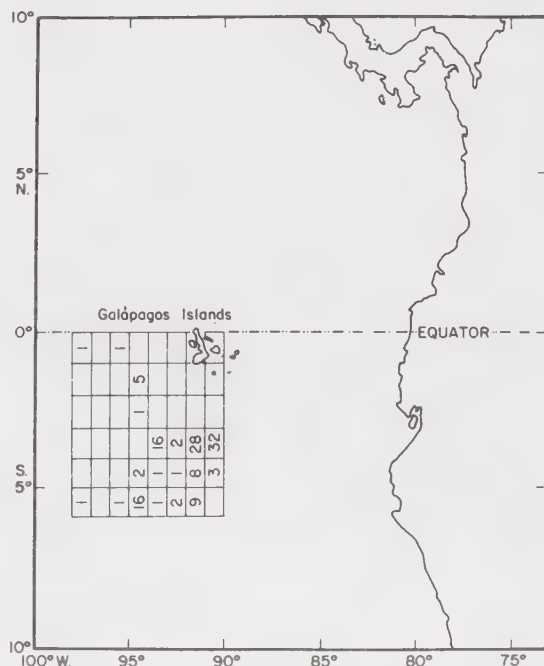


Fig. 9. Collection localities of 131 adult specimens of *Stenella attenuata* used in analysis of total length.

Table 4

Collection data for whole frozen specimens of *S. attenuata* from below the equator and west of 90° W longitude. Museum of Comparative Zoology number in parentheses.

Specimen no.	Locality (lat./long.)	Date	Sex	Length (cm)
1. DBF 014 (57257)	5° 05' S/94° 26' W	31 Oct. 76	F	171
2. DBF 015 (57258)	"	"	F	186
3. DBF 016 (57259)	"	"	M	176
4. DBF 018 (57260)	"	"	F	188
5. DBF 019 (57261)	"	"	F	188
6. DBF 021 (57262)	"	"	F	190
7. DBF 022 (57263)	"	"	F	189
8. DBF 023 (57264)	"	"	M	183
9. DBF 025 (57265)	"	"	F	188
10. DBF 027 (57266)	"	"	M	173
11. DBF 028 (57267)	"	"	F	179
12. DBF 029 (57268)	"	"	F	189
13. DBF 030 (57269)	"	"	M	204
14. DBF 032 (57270)	"	"	M	174
15. DBF 033 (57271)	"	"	F	177
16. DBF 034 (57272)	"	"	F	191
17. DBF 037 (57273)	5° 25' S/92° 33' W	4 Nov. 76	F	170
18. DBF 039 (57274)	"	"	F	187
19. DBF 040 (57275)	"	"	M	193

While the specimens analyzed here were nearly all collected in the single 5-degree block just southwest of the Galapagos, the distribution of reliable records of *S. longirostris* (Fig. 12) suggests a range extending south to about 12° S and from near the coast of South America west to at least about 103° W. Spinners observed in January 1977 at 11° 30' S latitude, 93° 48' W longitude on a research cruise of the R/V *David Starr Jordan* exhibited the typical "southwestern" color pattern (field notes of B. Lee). Sightings further to the west leave open the possibility that the distribution may be continuous with the range of spinner dolphins around the Marquesas Islands and elsewhere in the south Pacific. Specimens from the Marquesas and Tuamotus show affinities to the present specimens in that they are in some characters intermediate between the typical whitebelly and Hawaiian states, based on examination of photographs and sketches of several specimens collected by R. Costello and J. D. Bryant in that area in 1970 (K. S. Norris, University of California, Santa Cruz, pers. comm.). There is a near hiatus in records just below the Galapagos (Fig. 14), and a line drawn at 1° S latitude is a reasonable provisional northern boundary for the stock and the possible management unit. Since the range probably extends east to near the coast of South America, a better name for the stock than "southwestern spinner dolphin" is "southern spinner dolphin".

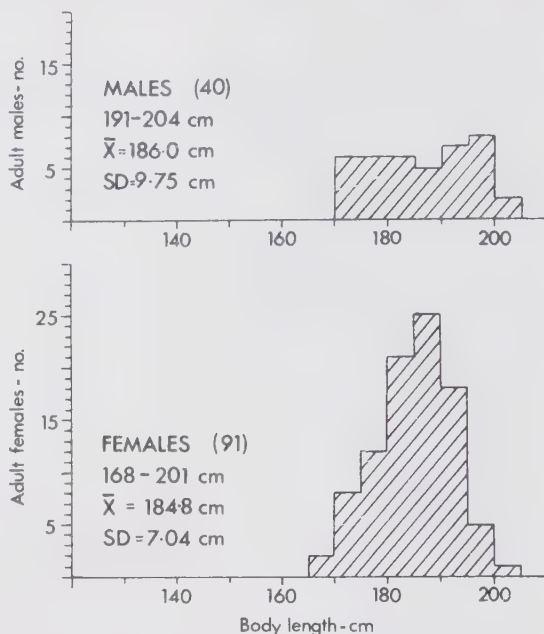


Fig. 10. Total length of adult spotted dolphins from south of the equator and west of 90° W longitude.

Table 5

External measurements (in cm) of adult spotted dolphins from south of the equator and west of 90° W longitude. Males with testis weight greater than 100 g, epidymis included (Perrin *et al.*, 1976).

Measurement	Sample size	Range	Mean	Standard deviation
Total length				
(M)	2	193-204	184.1	7.27
(F)	13	169.8-190.9		
Tip of snout to center of eye	15	25.0-28.4	27.2	0.86
Tip of snout to apex of melon				
(M)	2	8.4-10.8		
(F)	13	9.0-11.8	10.1	0.76
Length of gape	15	21.2-24.6	23.4	0.87
Tip of snout to blowhole	15	25.1-27.5	26.3	0.70
Tip of snout to anterior insertion of flipper	15	34.7-40.5	38.3	1.63
Tip of snout to tip of dorsal fin				
(M)	2	112.4-117.3		
(F)	13	73.1-111.1	104.3	9.59
Tip of snout to umbilicus	15	80.9-91.6	88.2	3.50
Girth at axilla				
(M)	2	82.5-86.5		
(F)	13	77.0-86.0	82.7	2.86
Flipper length to axilla	15	16.0-21.1	18.1	1.22
Fluke span				
(M)	2	42.0-44.0		
(F)	13	35.5-44.5	40.4	2.21

Table 6

Skeleton measurements (in mm) and meristics of adult spotted dolphins, *S. attenuata*, from south of the equator and west of 90° W longitude. Numbering system follows Perrin (1975a). Criteria of adulthood as for *S. attenuata* in Table 3.

Variable	Sample	Range	Mean	Standard deviation
1. Condylbasal length	17	382-414	398.9	8.98
2. Rostrum length	17	228-257	239.8	7.24
3. Rostrum width at base	17	79-91	84.4	3.10
4. Rostrum width at 60 mm	17	54-62	58.2	2.10
5. Rostrum width at midlength	17	38-46	43.8	2.10
6. Premaxillary width at rostrum mid-length	17	20-25	23.2	1.33
7. Rostrum width at ¼ length	16	25-34	29.6	2.22
8. Rostrum tip to external nares	16	266-295	279.5	8.61
9. Rostrum tip to internal nares	16	270-291	282.3	6.64
10. Preorbital width	17	148-160	152.7	3.83
11. Postorbital width	17	167-178	170.6	3.65
12. Least supraorbital width				
13. External nares width	17	40-47	43.1	2.58
14. Zygomatic width	17	166-178	169.8	3.98
15. Greatest width of premaxillaries	17	62-73	67.4	2.95
16. Parietal width	17	125-147	137.4	5.62
17. Braincase height	17	89-104	94.1	3.46
18. Braincase length				
(M)	5	110-116	113.8	2.48
(F)	12	103-118	111.2	3.29
19. Posttemporal fossa length	17	59-70	63.9	3.05
20. Posttemporal fossa width	17	45-57	50.6	3.29
25. Orbit length	17	45-50	47.9	1.61
26. Internal nares width	17	46-52	49.1	1.74
32. Upper tooth row length	17	194-221	205.4	6.58
33-36. Teeth (no.) U.L. U.R.	19 19	38-45 37-45	40.2 40.3	2.33 2.56
L.L. L.R.	18 18	35-43 36-42	38.7 38.6	1.97 1.85
37. Lower tooth row length	17	189-219	200.5	7.31
38. Ramus length	17	324-360	338.7	8.30
39. Ramus height	17	54-60	56.3	2.25
48. Thoracic vertebrae (no.)	19	15-17	16.1	0.70
49. Lumbar vertebrae (no.)	19	17-21	19.2	1.08
50. Caudal vertebrae (no.)	19	34-39	36.8	1.34
51. Total vertebrae (no.)	19	78-82	79.1	1.14

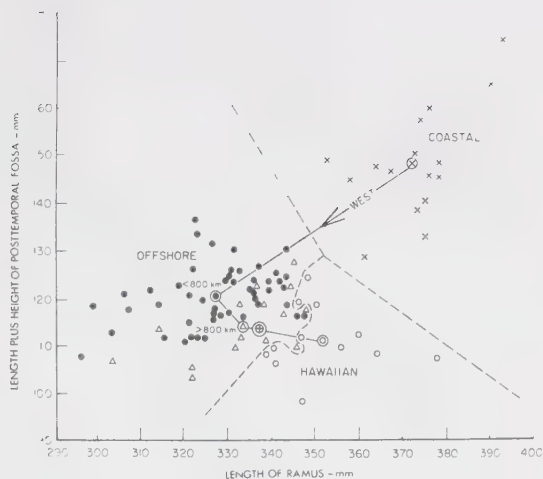


Fig. 11. Geographical variation in the skull of the spotted dolphin (from Perrin, 1975a), with mean for "southwestern" series (circled cross). Other sample means circled. Offshore specimens divided into two series, from less than and from more than 800 km from nearest point on the coast of the Americas. Arrow indicates relative location of coastal, offshore and Hawaiian series.

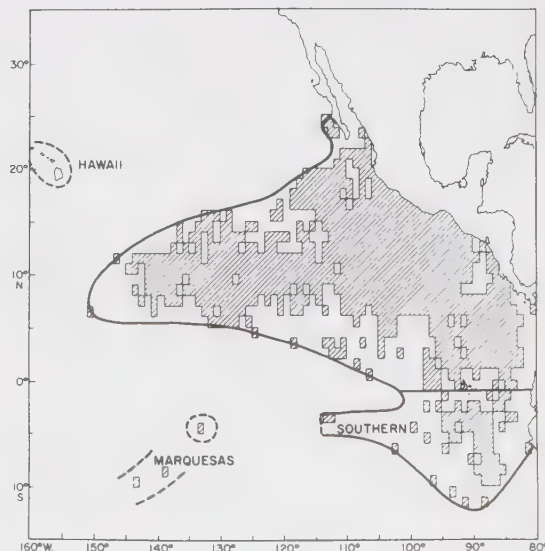


Fig. 12. Known range of *Stenella longirostris* in the eastern tropical Pacific (data from the tuna fishery, research cruises and other unpublished sources), with recommended northern boundary for possible southern management unit.

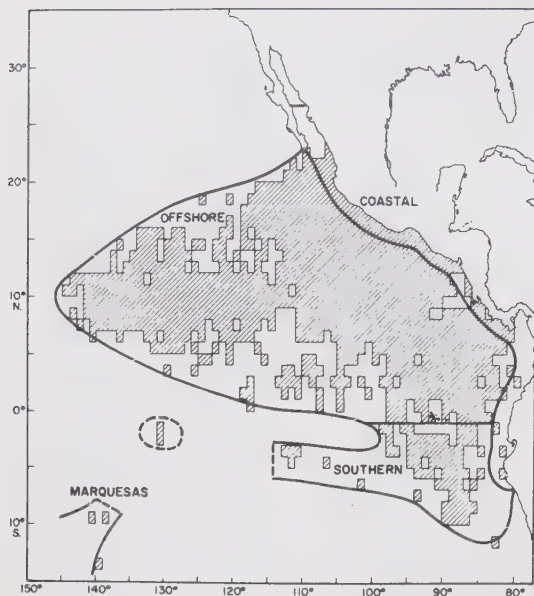


Fig. 13. Known range of *Stenella attenuata* in the ETP (data from tuna fishery, research cruises and other unpublished sources), with recommended northern boundary for possible southern management unit.

A very similar situation appears to exist for the spotted dolphin. The differences in morphology between the animals from below the equator and those to the north suggest some degree of isolation of the southern portion of the known distribution of the species in the eastern tropical Pacific, and a "southern" population can be defined (based again on a near hiatus in records, Fig. 13). This population or stock should be considered as a possible management unit.

The possibility that the modal differences between the populations in one or both cases are due to differential exploitation (perhaps affecting age and length at maturity) cannot be completely eliminated. However, it is unlikely, in that the size difference relationship is opposite in the two species; for one the southern form is larger, for the other it is smaller. It appears more likely the differences are genetically based. Such differences have been encountered in every adequate (using large samples and an array of characters) morphological comparison of populations of small cetaceans (Perrin, 1975a).

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NOTES

EFFECT OF SWIMMING SPEED ON THE
EXCESS TEMPERATURES AND ACTIVITIES
OF HEART AND RED AND WHITE MUSCLES IN
THE MACKEREL, *SCOMBER JAPONICUS*

Body temperatures of most fish typically are about the same as the water in which they swim for much of the heat generated by muscular activity is ducted away via the circulating blood and lost by convection at the gills and body surface.

Some scombrids and lamnid sharks conserve muscle heat using countercurrent vascular heat exchangers (retia mirabilia) so that temperatures are maintained significantly above ambient in the brain, eyes, red and white swimming muscles, and viscera (Carey et al. 1971; Stevens and Fry 1971; Linthicum and Carey 1972; Graham 1973). In other fishes lacking these heat conserving devices, only small temperature excesses above ambient have been recorded, but rarely more than 1°C (Stevens and Fry 1974). Since heat production must depend primarily on work output by the locomotor musculature, we have examined effects of swimming speed on the magnitude of the small temperature excesses in a "cool" scombrid not equipped with the retia exchangers, the mackerel, *Scomber japonicus* (locally the Pacific mackerel = chub mackerel).

Another important question concerning scombrid locomotion is how contractions of red and white muscle fibers are staged as swimming speed increases. It is generally thought that red muscle provides power for cruise swimming and that white muscle functions in "burst" swimming (Rayner and Keenan 1967). Red muscle is predominately aerobic and utilizes fatty acids as the major energy source whereas white muscle (which uses glycogen) usually functions anerobically (Gordon 1968; Bilinski 1974). The second objective of our study was to determine how heart rate and red and white muscle activity of *S. japonicus* are affected by swimming speed. For this purpose, electrodes were implanted into the pericardial space and in swimming muscles of fish so that simultaneous records of electrocardiograms (ECG's) and red and white electromyographs (EMG's) could be obtained.

The genus *Scomber* is a primitive member of the family Scombridae (Kishinouye 1923). It has a

fusiform shape, is less heavily bodied than the skipjack tuna, *Katsuwonus pelamis*, and other tunas, but shares several characteristics with warm-bodied species; they swim continuously (swim bladders are reduced or absent), have high rates of oxygen consumption (Baldwin 1923; Hall 1930), and have high blood hemoglobin levels (Greer-Walker and Pull 1975). They are also obligatorily dependent upon ram gill ventilation as adults (Roberts 1975) and have large gill surface areas with a high diffusion efficiency (Hughes 1966; Steen and Berg 1966).

Materials and Methods

Surgical Procedures and Swimming Experiments

The general procedure was to implant either thermocouples or cardiac (ECG) and muscle (EMG) electrodes into mackerel which were then placed in a Blažka-Fry tunnel respirometer (12 cm i.d.) to swim at controlled velocities. Fifteen specimens (35-40 cm fork length (FL); 0.38-0.62 kg) were obtained from regularly replenished and maintained mackerel stocks at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA. After netting, each fish was anesthetized in a large basin of oxygenated seawater containing 0.2 g/l of tricaine methanesulfonate (Crescent Research Chemical, Inc.)¹ and placed on an operating table where its gills were perfused continuously with a fast flow of oxygenated seawater containing a small amount of the same anesthetic (0.08 g/l). Thermocouples (0.127 mm in diameter copper constantan, polyvinyl chloride insulation) or electrode pairs (hooked, 0.07 mm in diameter stainless-steel, epoxy insulated) were implanted within the pericardial cavity just posterior to the ventricle, and in red and white muscles just under the leading edge of the second dorsal fin.

The white muscle thermocouple tip was placed midway between the vertebral column and the lateral edge of the body at the level of the horizontal midline. Preliminary dissections confirmed that red muscle in *S. japonicus* occurs in bands

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

that are concentrated below the skin along the lateral midline and become thicker posteriorly (see also Kishinouye 1923, fig. 16; Braekkan 1959, fig. 1). To ensure that the tip of the red muscle thermocouple would remain in place, the wire was passed from near the second dorsal fin obliquely through white muscle and then into the thin red muscle band. Once inserted, its position was easily verified by gentle fingertip probing.

To facilitate positioning of the two muscle thermocouples, 3-4 cm deep holes were tapped with a 20-gage hypodermic needle. The heart thermocouple was passed into the pericardial cavity through a 17-gage needle that was subsequently withdrawn. All wires were anchored in place by skin sutures. Wire leads (1 m long) to the recorder were lap wound together, passed posteriorly, and sutured to the dorsal midline near the finlets to prevent tangling around the tail. Implanting required about 15 min after which the fish was transferred to the respirometer swimming tube where aerated water was circulated over the gills by the driving impeller at a slow speed.

Two hours recovery from anesthesia and a brief period of swim training was required before a fish could maintain station in the tube and regulate swimming speed in response to water flow. This time delay also allowed stabilization of tissue temperature at ambient conditions following surgery.

Adaptation to the swimming chamber was carried out at a basal swimming speed which is 1.5 BL/s (body lengths per second) for *S. japonicus* (Magnuson 1973). This speed is also just above the velocity required for sustained ram gill ventilation (Roberts 1975). Flow rates in the respirometer were calibrated with a ducted flowmeter (Marine Advisors, Inc. model B-7C) and controlled by altering the applied armature voltage to the impeller pump motor. Eight fish were used for excess temperature measurements and seven were used to monitor EMG (4) and ECG (3) patterns.

Calibration Procedures

Thermocouples were made by soldering together the twisted bared tips of the copper and constantan wires and sealing them with epoxy cement. The three tissue thermocouples and a reference thermocouple (for respirometer water temperature) were each connected in series (constantan leads) to an ice-bath reference couple (0°C) and to an RS Beckman Dynograph (copper leads)

through a high-quality, shorting rotary-switch. This arrangement permitted rapid switching between thermocouples without opening the recorder circuit. Thermocouples were standardized in a water bath at $20^{\circ} \pm 0.05^{\circ}\text{C}$ before and after each trial.

Paired electrodes for recording ECG's and EMG's were prepared and implanted (in the same sites used for thermocouples) as described by Roberts (1975). The ECG and EMG signals were preamplified using high impedance, probe amplifiers (Grass, P511DR) to improve the frequency response of the RS Dynograph.

Seawater was kept continuously flowing through the respirometer tube and ambient temperature was maintained within 2.0°C in each experiment by mixing warm and cold seawater at the outlet taps of the laboratory seawater system. Over the 2-mo course of experiments, respirometer temperatures ranged from 16° to 22°C .

Results

Changes in excess tissue temperatures that accompany increased swimming speed in the mackerel are best seen in a particularly successful trial with fish number 6 (Figure 1). Similar, but somewhat variable records of heart, and red and white muscle temperatures were obtained for all fish (Table 1).

While cruising at low speeds, excess temperatures reached a maximum of about 0.3°C in the red and white muscles, but doubled within 3 min swimming at enforced higher speeds (3.2-4.5 BL/s). Excess temperatures recorded in the heart averaged about one-half of the excess developed in muscles at all swimming velocities. When swimming speeds were reduced once again to slow cruising, excess temperatures returned to pre-burst levels within 8-15 min.

During bouts of prolonged high-speed swimming (5-6 min), water in the swimming tunnel was warmed about 1°C due to frictional heating even though a continuous exchange of seawater was maintained from the supply tap (about 15 l/min). This thermal error was minimized by rapidly accelerating the fish from slow cruising to its predetermined, burst-swimming velocity. In Figure 1 for example, the fish was accelerated from 1.4 to 3.9 BL/s in about 5 s followed by sustained swimming for 3 min, and then rapidly decelerated to 1.4 BL/s. Equilibration of tissue thermal excess (i.e., generation minus dissipation) occurred in most

FIGURE 1.—Temperature excess in the heart and in red and white muscles recorded from *Scomber japonicus* no. 6 (35 cm FL, 0.45 kg) swimming at speeds from 1.4 to 3.9 BL/s. Arrows indicate timing and direction of speed changes. Ambient temperature, 19.5°-19.6°C.

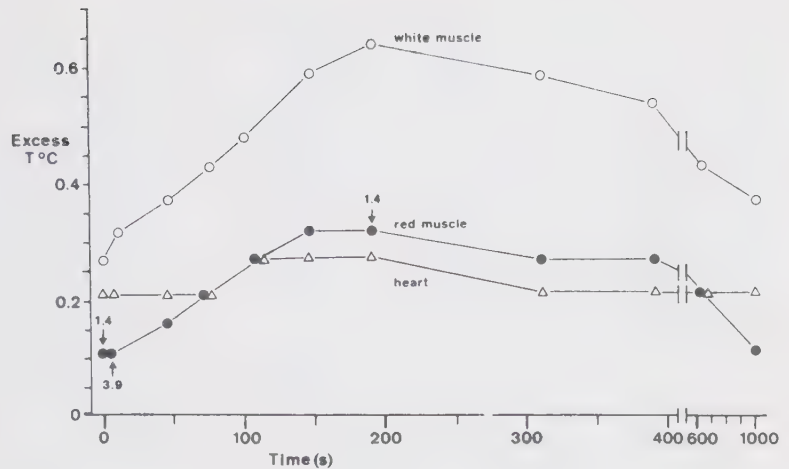


TABLE 1.—Temperature excesses as ΔT (°C) recorded for seven *Scomber japonicus* swimming at basal and moderately fast speeds in body lengths per second (BL/s).¹

Item	Fish number							Mean
	1	2	3	4	6	7	8	
Fork length (cm)	35.6	39.2	38.9	38.1	35.0	36.3	34.3	36.8
Weight (kg)	0.54	0.62	0.59	0.55	0.45	0.58	0.39	0.53
Highest ΔT at basal speed (1.3-1.9 BL/s) in:								
Red muscle	0.2	0.1	0.2	0.2	0.2	0.3	0.5	0.24
White muscle	0.2	0.3	0.3	0.2	0.4	0.3	0.3	0.29
Heart	0.0	0.3	0.1	0.1	0.2	0.2	(²)	0.15
Highest ΔT and swimming speeds (BL/s) in:								
Red muscle	0.9 (4.2)	0.75 (3.2)	0.55 (3.7)	0.85 (4.2)	0.3 (3.9)	0.5 (3.8)	0.8 (4.3)	0.66 (3.9)
White muscle	0.75 (4.2)	0.8 (3.2)	0.65 (3.7)	0.6 (3.9)	0.65 (3.9)	0.3 (3.8)	0.7 (4.3)	0.64 (3.9)
Heart	0.45 (4.2)	(²)	(²)	0.4 (4.5)	0.25 (3.9)	0.25 (3.8)	(²)	0.34 (4.1)
Maximum trial speed (BL/s)	4.2	3.2	3.7	4.5	3.9	3.8	4.3	3.9
Water temperature, range (°C) ³	16.1-17.0	16.5-17.0	16.8-17.8	17.1-17.5	19.5-19.6	20.5-21.0	21.1-21.8	

¹Fish no. 5 omitted because it would not swim in the respirometer tube.

²Thermocouple malfunction.

³Starting temperature is that of the seawater supply from mid-June to mid-July.

cases within the 3-min swimming bouts. Although the thermal excess was greater in white muscle of fish number 6 (Figure 1), mean maximum temperature excesses recorded in red and white muscles of the seven mackerel were about the same (Table 1).

Variability observed in excess temperature measurements seems attributable to different performances of individual fish. Some specimens had more body fat than others and did not swim steadily. Others were affected by the trailing thermocouple cable as evidenced by their tail-beat patterns. The cable also added drag which reduced speed but probably increased total heat production at a specific speed. None of the fish trailing thermocouple cables could swim steadily above 5 BL/s, whereas fish trailing the thinner ECG and EMG

cables could maintain a speed of 6 BL/s. Some of the variability in recorded thermal excesses may have also been due to the slightly differing locations of thermocouples in each fish. In addition, trauma due to thermocouple insertion, which probably interrupts normal blood flow locally may have been a factor influencing thermal convection. In a few cases, thermocouple signals changed abruptly possibly because of insulation failure at the tip due to rapid body flexing of fishes at higher swimming speeds.

A wide range was found in heart rates of mackerel cruising at 1-1.5 BL/s (mean, 106; range, 80-140 beats/min). With acceleration to 4-5 BL/s, the mean heart rate increased by 54% (mean, 130; range, 112-150), but rapidly returned to the resting rate within a few minutes of deceleration.

The EMG's demonstrate that both red and white muscle fibers contract synchronously while the mackerel swims at 2 BL/s (Figure 2). At slower velocities, even below basal speed, both red and white fibers were active during each tail-beat cycle. With acceleration to velocities above cruising, rates and amplitudes of both red and white EMG's showed proportionate increases; red muscle EMG's reached maximal amplitude between 3 and 4 BL/s. White muscle EMG's of the first mackerel tested appeared to increase in amplitude more than red muscle, and in proportion to velocity up to the highest speed at which the fish could swim steadily (about 6 BL/s). However, subsequent records obtained from three other fish did not confirm a consistent pattern of amplitude development with swimming velocity in the two fiber types. Variations in EMG amplitudes of single tail-beat cycles were commonly found in the recordings of all the fish from both red and white muscles at all swimming speeds. This is evident in the 1-s records for the fish in Figure 2. In this case, amplitude variability was more apparent at 5.9 BL/s because the fish's swimming became erratic—characterized by asymmetrical tail beats (unsteady or dart swimming). High-speed bilateral recording as used by Hudson (1973) would have aided the analysis. Figure 2 also shows that large bursts in white muscle sometimes accompany small bursts in red muscle, but confirmation of interactive contractile events in red and white muscles was not attempted.

Discussion

Body Temperatures

This study shows that *Scomber japonicus*, a strong continuous swimmer, does not develop large temperature excesses in its tissues while swimming at basal (1.3-1.9 BL/s) or sustainable (3-5 BL/s) speeds. Temperature excesses measured in the heart and in red and white muscles of this fish never exceeded 1°C and thus are not different from values typically found in species without specialized heat-conserving retia mirabilia (Lindsay 1968; Carey et al. 1971; Stevens and Fry 1974).

At high speeds, the lowest thermal excesses measured for the mackerel were in the heart. It was not possible to discriminate between heat actually produced by increased cardiac activity and that transported to the heart either via the blood (i.e., convectively) or by conduction. Some heat production must occur in the heart, but its mass is small compared with the volume of blood pumped per unit of time. Thus much of the muscle heat is either dissipated at the body surface or is conducted very slowly to other tissues before it reaches the heart and gills. There are several reasons why muscle heat may not reach the heart in venous blood. First, blood warmed in active muscles would be cooled as it mixes with blood returning from metabolically less active tissues. Also some countercurrent heat transfer (i.e., from

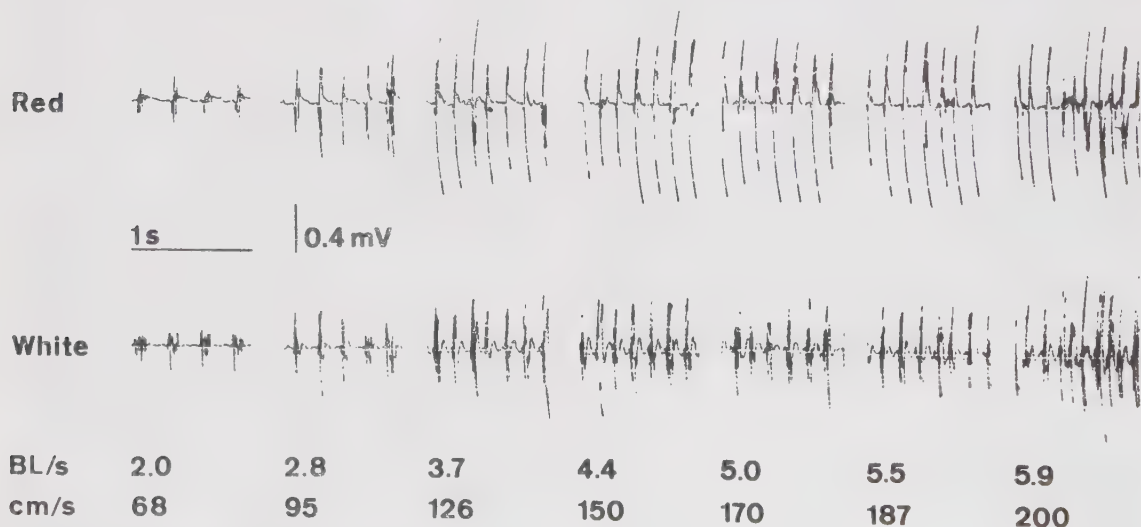


FIGURE 2.—Red and white electromyographs of a *Scomber japonicus* (34 cm FL, 0.39 kg) accelerating from 2.0 to 5.9 BL/s (68-200 cm/s) as indicated below EMG traces. Ambient temperature, 17°C.

a warm vein to an artery) between parallel and closely positioned arteries and veins (either segmental vessels or postcardinal vein and dorsal aorta) could reduce convective heat transport. For example, Stevens and Sutterlin (1976) demonstrated a mechanism of this type that transferred heat directly from afferent to efferent gill arteries in the sea raven, *Hemitripterus americanus*.

Fish body temperatures are not uniform. In most species, including the warm-bodied forms, the highest thermal excesses occur in deep muscles (both red and white) where body thickness is maximum (Lindsey 1968; Carey et al. 1971; Graham 1975). For this reason white muscle temperatures in the mackerel might be higher in more anterior regions of the body (i.e., at the first dorsal fin) where the white muscle mass and body thickness are greater. By contrast, higher temperatures in red muscle would not be expected because in *Scomber* this tissue is a thin band along the side of the body, only reaching maximum thickness as the body tapers toward the caudal peduncle (see figures in Kishinouye 1923 and Braekkan 1959).

Red and White Muscle Activity at Different Swimming Speeds

We were unable to determine a specific velocity where white muscle is recruited for swimming in the mackerel. At very low speeds, tail beats often became erratic or excessively strong. This may have been due to the added cable drag. Also, the basal speeds for fish in this study coincide with their minimum velocity needs for ram gill ventilation (Roberts 1975) which may have elicited struggling at slow speeds. Our EMG's do show low amplitude, synchronous potentials in both red and white muscles that were correlated with tail beats from very slow speeds up to about 2 BL/s. Amplitudes of EMG's in both muscle types seemed to reach a maximum for steady swimming at 3-4 BL/s, demonstrating that white fibers are active well within the range of sustainable cruising velocities for this species and that red muscle remains active at high speeds.

Neither patterns of motor innervation of red and white muscle fibers (focal or distributed) of scombrid myotomes nor the nature of their electrical responses seem to be known. Whether the compound potentials we recorded represent all-or-none spikes, abortive spikes, or rapid drifts in

membrane potentials (local potentials) following excitation, also is unknown.

We suggest that the amplitude changes recorded from both the red and white fibers as the fish accelerated represent fiber recruitment. White muscle electrodes were located close to the vertebral column, probably not closer than 1 cm to the lateral strips of red muscle, so detection of conducted red fiber potentials was unlikely. Amplitude variations detected in both muscle types during single tail-beat cycles was considerable. These variations were attributed to movement artifacts and possible drop-out of motor units nearby the electrodes.

A nearly completed dissertation study in one of our laboratories has demonstrated clearly that EMG's of red muscle in striped bass, *Morone saxatilis*, and in bluefish, *Pomatomus saltatrix*, also grade in amplitude with increasing swimming speed up to about 3 BL/s (M. A. Freadman, Graduate Student, Department of Zoology, University of Massachusetts, Amherst, MA 01003. Pers. commun., September 1977). But unlike *S. japonicus*, white muscle activity in these species does not appear until they reach burst-swimming velocities—a pattern of red and white muscle activation that resembles the herring (Bone 1975).

Red and white muscle fibers have different anatomical, physiological, and biochemical characteristics that relate directly to their roles in the swimming of different fishes (George 1962; Bone 1966; Bilinski 1974; Johnston et al. 1977). In some species red muscle functions over a wide range of speeds whereas white muscle is used only in burst swimming (Bone 1966). Staging in the activity of red and white muscles, that is the recruitment of white (mosaic red and white mixed as in salmonids; pink and white as in some carp) as velocity increases, has been observed in many species (viz., dogfish, Bone 1966; skipjack tuna, Rayner and Keenan 1967; rainbow trout, Webb 1971; Hudson 1973; coalfish, Greer Walker 1971; and carp, Johnston et al. 1977). The relative contribution of these muscle types to swimming no doubt relates to species-specific locomotory requirements for cruise swimming and maneuverability. However, more recently acquired data on this point show, as in *S. japonicus*, that white muscle fibers do often function at low, sustainable swimming speeds (e.g., in coalfish and carp) and thus are not exclusively reserved for high-speed burst swimming (Johnston et al. 1977).

For scombrids, which swim continuously and rely upon forward motion to ventilate their gills, the existence of a relatively high speed for the division of labor between red and white muscles, has been assumed primarily on the basis of work done by Rayner and Keenan (1967). These investigators concluded that in the skipjack tuna, red muscle alone powered cruise swimming and white muscle only became active at burst velocities. The initial objective of Rayner and Keenan's study was to demonstrate contractile properties of red muscle, and to this end they blocked white muscle activity (pentobarbital) and worked exclusively with tranquilized (propriopromazine) or sedated fish. Moreover, their specimens were restrained in a fixed position and artificially ventilated by perfusion tubes in the mouth. Thus the movements by these skipjack tunas that were identified as "low frequency swimming," were in fact only casually related to the swimming requirements for gill ventilation and hydrostatic equilibrium; both are controlling factors in normal swimming (Magnuson 1973; Roberts 1975).

Our results with *S. japonicus* contrast in that they show both red and white muscles function in low-speed swimming. Also, Dizon and Brill (A. E. Dizon, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812. Pers. commun., September 1977) recorded red and white EMG's from yellowfin tuna, *Thunnus albacares*, and found that white muscle activity begins at swimming velocities of <3 BL/s—a speed only slightly above the minimum for hydrostatic equilibrium and well below maximal burst capabilities (Magnuson 1973). These observations indicate that in fast-swimming scombrids, patterned staging of red and white muscle activity may differ in that activity begins in white fibers at very low speeds, and that both red and white muscle remain active throughout a wide range of sustainable speeds as well as at burst velocities. Implicit in this idea is the presence of a high scope for aerobic activity in scombrid white muscle which has been recently demonstrated for the skipjack tuna (Guppy et al. in press). Also required by the hypothesis are specializations in red muscle for high-speed contraction which is supported by the findings of Johnston and Tota (1974) that high levels of myofibrillar ATPase occur in the red muscle of bluefin tuna, *T. thynnus*.

What physiological advantage might be gained by a 1°C thermal excess during fast swimming?

Assuming a Q_{10} of 2 then a 10% increase in metabolism would afford about a 2-3% rise in swimming speed, but an insignificant change in overall swimming efficiency (Webb 1971). An interesting speculation is that the extensive heat-exchanging vascular network used for endothermy in the scombrids may have initially evolved to meet the high oxygen requirements of red and white myotomal muscle. More metabolic heat is produced during aerobic respiration and natural selection may have proceeded toward a vascular design that maximized oxygen delivery, yet augmented muscle function by conserving heat and insulating the swimming musculature from ambient conditions.

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Vertical Sections of Semimonthly Mean Temperature on the San Francisco-Honolulu Route: From Expendable Bathythermograph Observations, June 1966-December 1974

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ABSTRACT

Frequently repeated sections of expendable bathythermograph observations between San Francisco and Honolulu, taken by merchant vessels during the period June 1966 through December 1974, were analyzed to obtain mean seasonal cycles. Results are depicted in a set of semimonthly vertical sections of mean temperatures to 500 m and in a set of corresponding sections of 30-day mean temperature changes to 200 m. In addition, seasonal cycles at selected depths are included along with mean monthly vertical profiles for seven typical locations along the route.

The analyses reveal geographic and temporal facets of the mean thermal structure, including: 1) depth of the surface mixed layers in winter, 2) growth and decay of the seasonal thermocline, 3) decrease in depth of the permanent thermocline from Oahu to the California coast, 4) a region of temperature inversions or very weak vertical temperature gradients that develops between 50 and 100 m during the spring in the Transition Zone, and 5) the location and movement of warming and cooling regions during the year.

Vertical mixing appears to be the dominant process along most of the route for transmitting the annual surface warming and cooling cycle downwards to depths of 100 to 150 m. However, advective processes are active in the California Current.

Tables of semimonthly mean temperatures are given in an Appendix.

INTRODUCTION

Vertical sections of mean subsurface temperatures from the surface to 500 m, presented here, were derived from a time-series of sections of expendable bathythermograph (XBT) observations made from June 1966 through December 1974 by merchant ships between San Francisco, Calif., and Honolulu, Hawaii (Fig. 1). The observational program was developed by Saur and the data collected under the direction of the National Marine Fisheries Service (NMFS). With technical assistance from the Fleet Numerical Weather Central (FNWC), XBT systems were placed on merchant ships and observations were made routinely by the ship's mates. Saur and Stevens (1972) described the XBT system, observational procedures, and early projects for obtaining observations from cooperating ships.

Collection of subsurface temperature observations on the San Francisco-Honolulu route began when the first production models of the XBT system became available. The work started as a 1- to 2-yr feasibility and

development project on the use of the system aboard merchant vessels. It was then continued as an ocean monitoring project, and is now a part of a coordinated program among FNWC, NMFS, and NORPAX (North Pacific Experiment) programs to obtain XBT observations in the Pacific. The data are now routinely collected

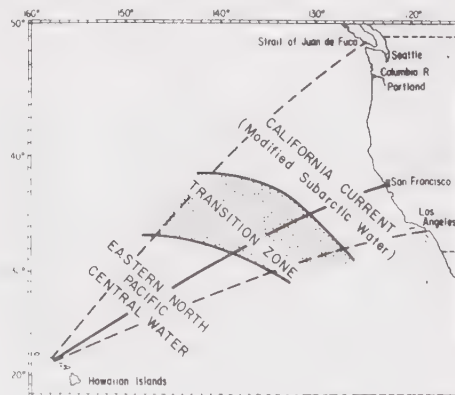


Figure 1.—Three great circle routes between Honolulu and U.S. west coast ports, on which frequent XBT observations have been made by cooperating merchant ships, and a schematic representation of the three upper ocean regimes in the area. Mean subsurface temperatures reported here are for the San Francisco-Honolulu route for which the longest time series—starting in June 1966—exists.

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and selected vertical sections of the temperature distribution, with individual XBT profiles, have been published regularly in *Fishing Information*⁶ since March 1972.

The ship routes between Honolulu and U.S. west coast ports cross the eastern limb of the major anticyclonic gyre of the North Pacific Ocean. If we confine our attention to the upper ocean, from the surface to a few hundred meters, we can identify three oceanic regimes: the California Current and the Eastern North Pacific Central waters separated by a Transition Zone (Fig. 1).

The waters in the California Current are mainly cooler, lower salinity waters of subarctic origin that are modified in their slow southeastward movement along the California coast. The Eastern North Pacific Central waters are warmer, higher salinity waters that occupy about the southwestern one-half of the route.

The Transition Zone is a complex region, not yet fully understood. In our region of interest it is bounded on the south and southwest by the subtropical front (Roden 1971, 1975). On the north and northeast it is bounded, respectively, by the subarctic front (Dodimead et al. 1963) and some type of southeastward extension of this feature, which LaFond and LaFond (1971) called the California Front. Saur (1974) described criteria for identifying these regimes from the XBT profiles, changes in slopes of isotherms in the vertical sections, and accompanying surface salinity observations. Laurs and Lynn (1977) discussed features of the Transition Zone from oceanographic observations made in June of several different years by fishery research vessels.

Mean temperatures presented here provide a base for study of temperature anomalies (Dorman and Saur 1977, 1978) and for further research on the relation of temperature variability to air-sea interaction and the changing environment of marine organisms.

METHODS

Observations

The time-distance distribution of XBT observations for the period June 1966 through December 1974 is shown in Fig. 2. The great circle distance from a reference point near Oahu was used for location. About 90% of the observations were made by ships on the great circle route. Some departures from the great circle track resulted from storms and the fact that tankers of Chevron Shipping Company generally followed a rhumb line (constant heading) course. For these observations taken at locations displaced from the usual route by 100 to 150 km, the use of great circle distance from Oahu tends to minimize temperature errors, because the general orientation of isotherms in the upper layers is northwest-

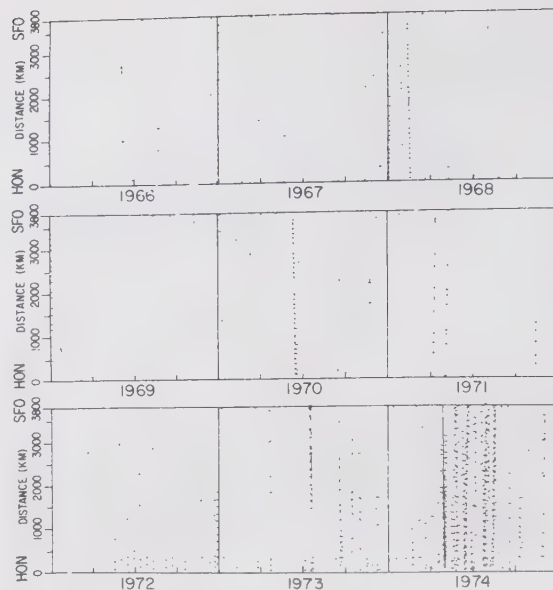


Figure 2.—The time-distance distribution of XBT observations on or near the San Francisco-Honolulu route from June 1966 through December 1974. Location of an observation is measured by its great circle distance from an offshore reference point (lat. 21°12'N, long. 157°42'W) near Honolulu.

southeast. The San Francisco end of our section is a point on the edge of the continental shelf a short distance south-southwest of the Farallon Islands and 3,800 km (2,050 n.mi.) from the reference point.

With the exception of the first year and one-half when only four observations per day were scheduled, the XBT observations were taken on a 4-h schedule related to the ship's watch, rather than at prespecified "stations." Thus the location of observations along the route differs from one section to another. Also, the distance between observations depended upon the ship's speed. Of those ships cooperating in the program, normal speeds were either about 16 to 17 kn or about 22 kn, so that the distance between observations was about 120 km (65 n.mi.) or 165 km (90 n.mi.), respectively. The slower ships would generally get 27 to 30 observations per transit and the faster ships about 17 to 20 observations. A few sections with more closely spaced observations for special studies were made when scientific personnel were aboard.

The frequency of sections reflects the growth and change in character of the project. With the exception of six sections made by oil tankers in the summer of 1970, all of the observations from the beginning of the project in June 1966 through January 1971 were made from one vessel, *Californian*, a bulk-cargo and container vessel of Matson Navigation Company. This 17-kn ship made a round trip about every 18 to 21 days, generally making observations on one 5-day leg only. During this period several gaps of 4 to 8 wk duration occurred because of ship repair schedules, short labor strikes, and equipment failures.

⁶*Fishing Information* is a National Marine Fisheries Service monthly publication, containing fishery advisory information and environmental charts for the equatorial and North Pacific Ocean. It is compiled and distributed by the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

A prolonged maritime strike in 1971 interrupted the series for two periods of nearly 3 and 5 mo each. A faster (22 kn) ship, *Hawaiian Enterprise*, made most of the sections in 1971 and 1972, resulting in more frequent sections but with greater spacing between observations. As a part of the International Decade of Ocean Exploration (IDOE) programs, we began instrumenting other ships in late 1972 for other routes, but which also would make sections irregularly on the San Francisco route. Using these ships, the frequency of sections on the San Francisco route was increased in 1973 and intense coverage was obtained in 1974.

For the entire period from June 1966 through December 1974 there was a total of 4,913 observations (Table 1). A number of the sections did not have complete coverage, with the coverage generally being poorest near either end of the route. This should be considered when interpreting the computer analyses which will be presented.

Instrumentation

The basic sensing and recording system used throughout the period was the Sippican XBT system. Progressive improvements were made in the recorder by the manufacturer—some partially due to the field experiences from this project—during the first few years, 1966-68. Since then, the recorder, with pressure sensitive paper and an option switch for 460 m (1,500 ft) or 760 m

(2,500 ft) depth recording, has remained essentially unchanged.

The XBT system initially installed aboard the *Californian* included an experimental digitizer (developed by FNWC) with analog signal input from a retransmitting slidewire in the XBT recorder and digital output onto a 5-level punched paper tape at depth intervals of slightly less than 3 m (Saur and Stewart 1967). This was a dual purpose output for testing radio transmission of data to FNWC and for subsequent computer conversion, ashore, onto magnetic tape for permanent archives. The digitizer system became unstable after April 1969 which made the output unsuitable for archiving data. Although commercial digitizing systems were tried with some of the new recorders installed on other ships in 1971 and 1972, all of the data used herein from May 1969 onward were derived from the analog traces.

Sippican model T-4 XBT probes (460 m) were used during the first 1.5 yr of the project. We switched to use of model T-7 probes (760 m) in November 1967, to try to minimize probe-to-probe temperature errors by correcting deep temperatures to a smoothed deep level temperature (e.g., 600 or 700 m). This plan proved to be unworkable because the deep level temperatures could be offset to warmer temperatures by insulation failures on the wire and such a bias could not always be recognized with certainty by examination of the analog traces or vertical sections. At a later date mesoscale eddies were discovered and appeared to have deep

Table 1.—Number of expendable bathythermograph (XBT) sections by cooperating ship and total observations by year on the San Francisco-Honolulu route.

	Year									Total sections
	1966	1967	1968	1969	1970	1971	1972	1973	1974	
Matson Navigation Co.										
<i>Californian</i>	10	15	18	15	15	5			6	84
<i>Hawaiian Enterprise</i>						4	18	19	26	67
<i>Hawaiian Citizen</i>									1	1
<i>Hawaiian Queen</i>									10	10
Chevron Shipping Co.										
<i>Idaho Standard</i>					3					3
<i>Washington Standard</i>					2					2
<i>McGarraill</i>					1					1
<i>Chevron Californian</i>							1	2	1	4
<i>Chevron Mississippi</i>							1	4		5
States Lines										
<i>Michigan</i>						1				1
<i>Idaho</i>						1				1
American President Line										
<i>President Cleveland</i>						1				1
Pacific Far East Line										
<i>Monterey</i>								2	1	3
<i>Mariposa</i>									9	9
U.S. Coast Guard										
USCGC <i>Midgett</i>								2		2
Total sections	10	15	18	15	21	12	20	29	54	194
Total observations	204	329	550	435	592	229	453	635	1,486	4,913

¹11-16 February 1968 section had two XBT drops at each 4-h interval.

²Includes one special section, 27 April-1 May 1974, with hourly observations by R. L. Bernstein and C. A. Collins.

temperature changes equal to or greater than temperature error of the probes manufactured in 1968 and later.

As the cost of probes rose in the early 1970's we returned to using T-4 probes. With the merchant ships the amount of wire on the probe was the limiting factor on depth of the XBT observation. We found that the manufacturer's safety margin of excess wire on the probe usually permitted a reliable determination of temperature to 500 m.

Initial Processing

The procedures for initial processing of the observations into digital form on magnetic tape evolved as the project developed.

As noted earlier, the XBT system used during 1966-69 aboard the *Californian* included an experimental digitizer with a punched paper tape output. Most of the observations through April 1969 were computer translated from this output, which was regularly calibrated with the manufacturer's test canister on the visit to the ships before and after each voyage. In cases of digitizer failure significant points were read by eye from the analog traces, as were all observations for May-December 1969. Some sets of observations from 1967 to 1968 were semiautomatically digitized by FNWC in the early stages of development of its XBT digitizing system for computer determination of temperature-depth inflection points.

When the NMFS Pacific Environmental Group (PEG) was established in Monterey, the 1970 and later observations were digitized on an analog-digital table, under the supervision of McLain and using the facilities and computers of FNWC. The digitizing procedures generally followed those used at FNWC, described by Dale and Stevens (1970), except as modified by McLain at PEG to handle the NMFS data separately from FNWC data, to digitize analogs from T-4 probes to 500 m, and to plot vertical sections.

Quality Control

Preliminary vertical sections of the distribution of temperature were constructed, at first by hand and later by computer, for quality control. Saur reviewed each data set for possible errors utilizing the preliminary sections, analog traces, and continuity from section to section. Locations of observations were plotted to help check positions and an independent check of time and distance between observations was made against the ship's speed. For observations through 1970, copies of marine weather logs on which positions of 6-h weather observations were logged independently of XBT logs were also used to correct time and position errors.

The data checks were made to eliminate large errors due to instrument failure not detected before digitizing. These were of several types: 1) erroneously high temperatures throughout a trace due to defective thermistors or insulation failure from the start, 2) insulation failure during the probe descent which would intro-

duce bias toward higher temperatures in the remainder of an analog record, and 3) slippage of the friction clutch on the chart drive, which occurred mainly in early years before we became more experienced with the XBT system. Corrections were made at a later time when temperature values were interpolated at 5-m intervals between the surface and 300 m and at 10-m intervals between 300 and 500 m depth, for the computer analysis of temperature fields.

Computational Procedures

The determination of the vertical sections of mean subsurface temperature presented herein involved three steps: 1) Conversion of observed temperatures from each section to temperatures on a standard grid; 2) computation of a seasonally varying mean at each grid point by least squares fit of 12-, 6-, and 4-mo harmonics; and 3) reconstruction of gridded temperature fields from the harmonics, spatial smoothing, and contouring of vertical sections. The computer programs used for this were adaptations by Eber of those he prepared at SWFC to map environmental variables in marine weather observations for presentation in *Fishing Information*.

1. Conversion to a standard grid.—It was previously mentioned that observations were not taken at the same predetermined location from section to section. The first step was to analyze observed values from each section to a standard rectangular grid, using a procedure from Eber's EDMAP⁶ (Environmental Data Manipulation, Analysis, and Plotting) program.

The grid was selected with a distance interval of 92.5 km (50 n.mi.) and a depth interval of 10 m. This resulted in a grid of 42 by 51 points representing a vertical section 3,800 km (2,050 n.mi.) by 500 m. Distance and depth were converted to grid coordinate units for the temperature analysis.

The procedure scanned the data list and fitted temperature values to the grid. Each observation contributed to the values at its nearest grid points according to an inverse weighting scheme based on distance from the observation to each of the grid points. The weighting factor decreased to zero at one grid length. If no observation was found within one grid length of a grid point, it was flagged as a "no data" point in that section.

The procedure can be viewed as a refinement of centering the observational data within 185-km (100 n.mi.) by 20-m blocks that have a 50% overlap between adjacent (both vertically and horizontally) blocks. However, if there is more than one observation within a block, each is weighted according to the distance to the center of the block and the number of grid points it will affect. (The

⁶Unpublished documentation of the EDMAP program is on file at the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

procedure gives somewhat greater weight to an observation near a grid point than would a weighting of $1/R^2$, where R is the distance in fractions of a grid length.) If there is only one observation within a unit grid area and there are no observations in any of the surrounding grid areas, the observed value would be assigned to each of the four nearest grid points.

The middate of the observations in a given section was assigned to its corresponding grid field for later use in determining harmonic coefficients. Thus the maximum time error for data at either end of the section would be about 2.0 to 2.5 days.

2. Least squares harmonic fit.—In order to establish a smooth mean seasonal cycle for each gridpoint, a least squares fit was made for the harmonic function

$$T_{i,j} = (A_0)_{i,j} + \sum_{n=1}^3 (A_n \cos n\omega t + B_n \sin n\omega t)_{i,j}$$

where $\omega = 2\pi/365$, t is the day of the year, and i and j are gridpoint indices. Robinson (1976) also used the first three harmonics of the Fourier function for time smoothing of monthly mean values of mechanical bathythermograph data (to 400 ft) for the North Pacific Ocean. Since our initial gridded fields were not distributed at equal intervals in time, the terms which normally disappear in harmonic analysis of evenly spaced data (due to orthogonality) are not zero when applying the least squares fit. Seven simultaneous equations for least squares fit were solved to determine the seven unknown constants to represent the mean temperature and the 12-, 6-, and 4-mo cycles.

To avoid overweighting certain years because of greater sampling frequency, a set of harmonic constants was determined for each of three time periods: June 1966–December 1970, 1971–73, and 1974. The first period was selected because of the consistency of the sampling mentioned earlier. The year 1974 was analyzed separately because of the unusually high-density sampling. The observations from 1971 and 1972 were considered as 1 yr and combined with 1973.

Constants from the three periods were weighted and combined by Dorman to provide the mean constants representative of the 1966–74 period. Weights assigned to the periods were as follows:

Period	Weight
June 1966–December 1970	4.5
1971–1973	2.0
1974	1.0

3. Vertical sections of mean temperature and mean temperature change.—Appendix 1 contains vertical sections of the mean temperature structure along the Honolulu–San Francisco route, to depths of 500 m, for 24

equally spaced times throughout a year. (For convenience of identification these are labeled as 01 January, mid-January, 01 February, etc., to mid-December.)

The data field for each of the 24 mean vertical sections was reconstructed from the harmonic functions at each grid point. Because the time smoothing by the least squares fit was independent from point to point, a spatial smoothing was applied to the grid field before contouring.

The spatial smoothing was done with one pass of a 5×5 point (370 km by 40 m) smoother in the EDMAP program. The smoother was a two-step numerical filter, after Shapiro (1970), which was mostly effective for reducing amplitudes of perturbations with wave lengths of less than about four grid lengths. Its response was zero at a wave length of two grid lengths, 0.45 at three grid lengths, and 0.75 at four grid lengths. The response was 0.96, or greater, at wave lengths of seven grid lengths or more.

The contouring part of the EDMAP program divided each grid square into 25 subsquares, whose corner values were determined by Bessel's central difference formula for double quadratic interpolation. The intersection of each contour with the boundary of a subsquare it transects was determined by linear interpolation. The isotherms were computer plotted and are reproduced herein, with drafting touch-up only for clarity of presentation. The isotherms were not changed subjectively.

The major changes in the seasonally varying mean temperature were found to occur in the upper 200 m of the water column. The figures of Appendix 1 also show the distribution of the "30-day" temperature changes for the upper 200 m. The changes were computed from the spatially smoothed data (described on page 7) and are centered on the date of the vertical section in the upper panel. Note that there is a 50% overlap between two consecutive temperature change charts.

4. Tables of mean temperature.—Mean temperature values, in °C, for selected depths and alternating grid points (intervals of 185 km) are presented in Appendix 2. The values are those reconstructed from the fitted harmonics for the given grid point (distance and depth) and extracted before the grid was spatially smoothed for contouring. The tables are identified as 01 January, mid-January, etc., to mid-December, as were the vertical sections of Appendix 1.

RESULTS

This section discusses some of the general features of the mean temperature distributions in Appendix 1. Further, we have selected seven locations, each of which has vertical temperature structure and cycles characteristic of a part of the route. For each of these, Figure 3a–g shows the seasonally varying mean temperature for eight depths from the surface to 500 m, and Figure 4a–g shows the mean monthly vertical profiles of temperature for the warming and cooling periods.

Annual Cycles

At the surface the annual period is predominant at all locations (Fig. 3a-g). The annual range was smallest (about 4°C) near Oahu, largest (about 7°C) in the Transition Zone, and again smaller near the California coast (about 5°C). From near Oahu to the California front, the cycles at 50 m diminished in amplitude and the summer maximum lagged that at the surface by 1 to 2 mo. At the low salinity core of the California Current (Fig. 3f) the summer maximum penetrated almost simultaneously from the surface to 200 m. In the inshore area, California Current (Fig. 3g), the temperature range at 50 m was small (about 1°C). Here the minimum and the maximum temperatures lagged those at the surface by about 4 mo, and appear to be related to the occurrence of upwelling and the subsurface countercurrent, respectively.

Mixed Layers and Thermoclines

The surface mixed layers reach their maximum depth in winter, mid-February through early April, Appendix 1. Depths of the mixed layers were generally at least 100 m, except they decreased to 75 m near California. They were deepest, about 150 m, in the central part of the section (2,000 to 2,200 km) in the neighborhood of the subtropical front.

We consider the permanent thermocline to be the region of the maximum vertical temperature gradient in winter (January through March); vertical sections of Appendix 1 and profiles of Figure 4. In the western half of the section it was deeper (200 to 250 m) and warmer (15° to 17°C) than in the California Current region where it

lay at depths of 100 to 120 m and had temperatures of 11° to 13°C. The seasonal thermoclines are formed by warming in spring and summer (May through September) and are generally confined to the upper 50 to 100 m which are vertically mixed in winter. In the California Current region the seasonal thermocline merged with the permanent thermocline into a single feature, whereas in the Transition Zone the two thermoclines were separated in the spring by temperature inversions (next section) and later by a near isotherm (vertically isothermal) layer, Figure 4d. The latter was particularly evident in the summer (July through August) sections by the steeper slope of the 15°-19°C isotherms at depths from 50 to 150 m at distances of 2,000 to 3,000 km from Honolulu. In the Eastern North Pacific Central waters from Honolulu to near 1,800 to 2,000 km along the route, a layer of weak vertical temperature gradient occurred between the seasonal and permanent thermoclines.

Temperature Inversions

A characteristic feature found by Saur (1974) in the individual profiles in the Transition Zone (between 2,000 and 3,000 km from Honolulu) was the occurrence of complex vertical thermal structure, especially in the spring months. The thermocline would often be interrupted by isothermal layers and temperature inversions appeared in some profiles. These were attributed to interleaving, by horizontal mixing, of layers of cool, low-salinity water with warmer, higher salinity water of nearly the same density. These features usually are relatively small scale and transient, so that during our computation of means, they were generally smoothed out. However, some

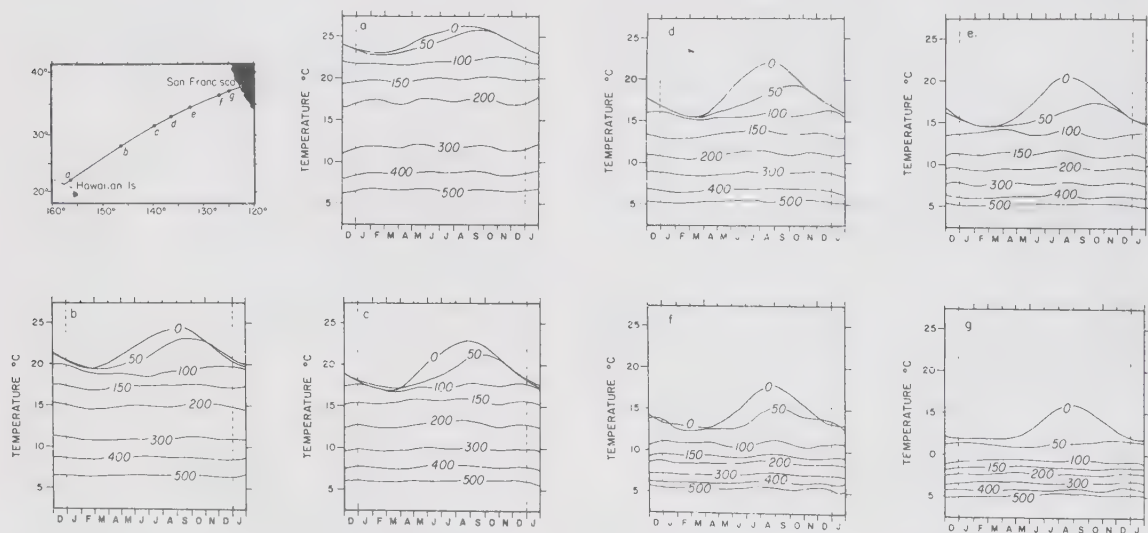


Figure 3.—Station position chart and mean temperature cycles at selected depths (meters) for seven typical locations, great circle distances from offshore reference point (lat. 21°12'N, long. 157°42'W) near Honolulu, and geographic coordinates: a. Near Oahu: 185 km (100 n.mi.); lat. 22°10'N, long. 156°15'W. b. Eastern North Pacific Central Water: 1,390 km (750 n.mi.); lat. 28°17'N, long. 146°20'W. c. Subtropical front: 2,130 km (1,150 n.mi.); lat. 31°39'N, long. 139°42'W. d. Transition Zone: 2,500 km (1,350 n.mi.); lat. 33°12'N, long. 136°12'W. e. California front: 2,870 km (1,550 n.mi.); lat. 34°39'N, long. 132°35'W. f. Low salinity core, California Current: 3,430 km (1,850 n.mi.); lat. 36°36'N, long. 126°55'W. g. Inshore region, California Current: 3,615 km (1,950 n.mi.); lat. 37°12'N, long. 124°59'W.

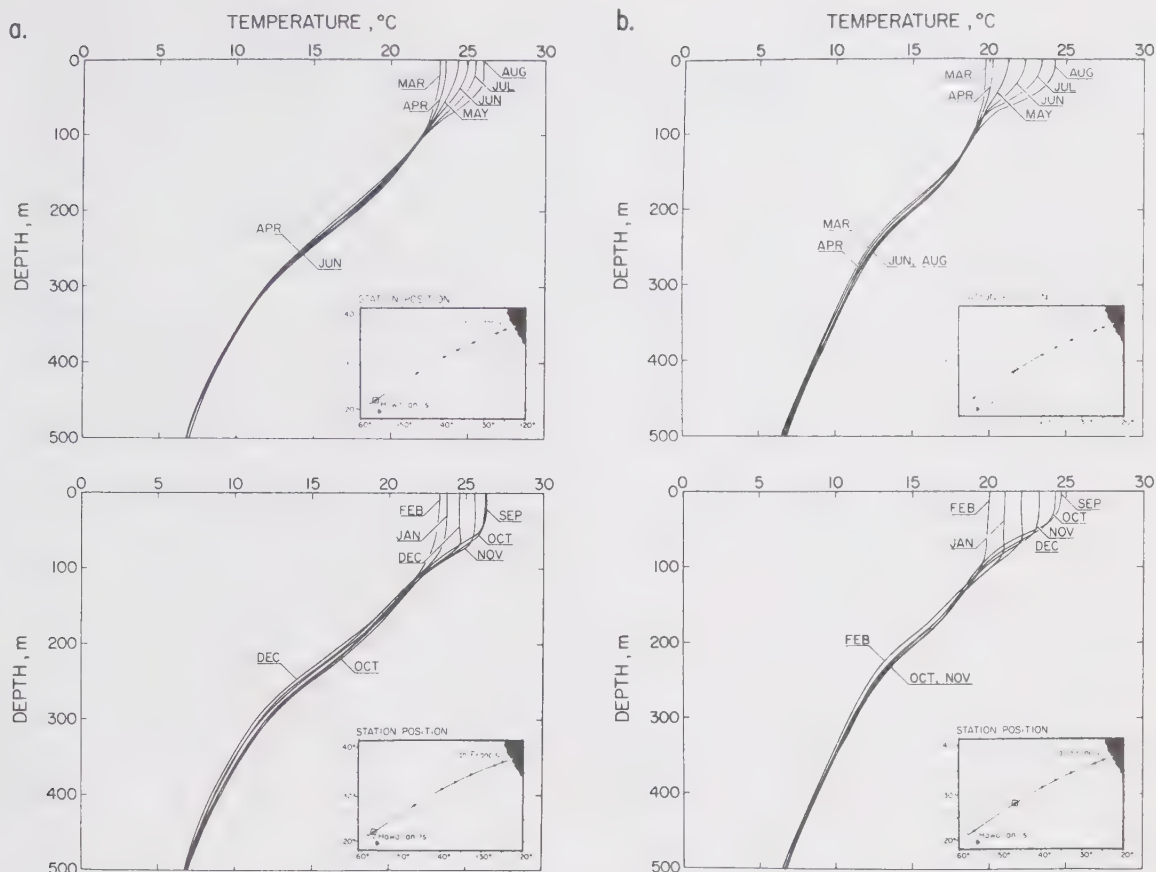


Figure 4.—Monthly profiles of mean temperature ($^{\circ}\text{C}$), for warming and cooling periods at seven typical locations (shown by diamond on inset chart); distance from offshore reference point near Honolulu and geographic coordinates as in Figure 3. a. Near Oahu. b. Eastern North Pacific Central Water. c. Subtropical front. d. Transition Zone. e. California front. f. Low-salinity core of the California Current. g. Inshore region of California Current.

temperature inversions remained in the vertical sections of Appendix 1, e.g., the 15°C isotherm in the 01 April section, the $15^{\circ}\text{--}17^{\circ}\text{C}$ isotherms in the mid-April section, the $16^{\circ}\text{--}17^{\circ}\text{C}$ isotherms in the 01 May section, and the 16°C isotherm in the mid-May section. It appears that, on the average, when surface warming begins in the spring and vertical mixing is suppressed, the warmer, higher salinity Eastern North Pacific Central waters spread toward the California coast around 100 m, under-running the low-salinity, modified subarctic waters which are still cool around 50 m.

In winter months, e.g., mid-January section of Appendix 1, there appeared to be a temperature maximum at the base of the mixed layer between 1,200 and 3,000 km along the section. From an examination of individual profiles it was found that these were not typical of usual conditions. There was almost always an isothermal layer to the top of the thermocline. The apparent maximum resulted from the tendency of the three harmonics to give near-surface temperatures for this area in winter which

were slightly low, 0.1° to 0.2°C . The weak horizontal temperature gradients and vertical exaggeration of the section, amplified the effect in the computer contoured sections.

Structure Below the Permanent Thermocline

Below the permanent thermocline, the slopes of the isotherms can be used to separate the section into two regions. The 10°C isotherm is typical. In the western part of the section from Honolulu to about 1,800 km it generally changed depth by less than 50 m, i.e., the slope was less than 3 m/100 km. In the eastern part of the section, from a point at 2,200 km on the section to near San Francisco (3,800 km) the depth of the 10°C isotherm decreased by 150 to 200 m, or a slope of greater than 9 m/100 km. The smaller slopes are associated with the Eastern North Pacific Central waters, while the steeper slopes were associated with both the California Current and Transition Zone regions.

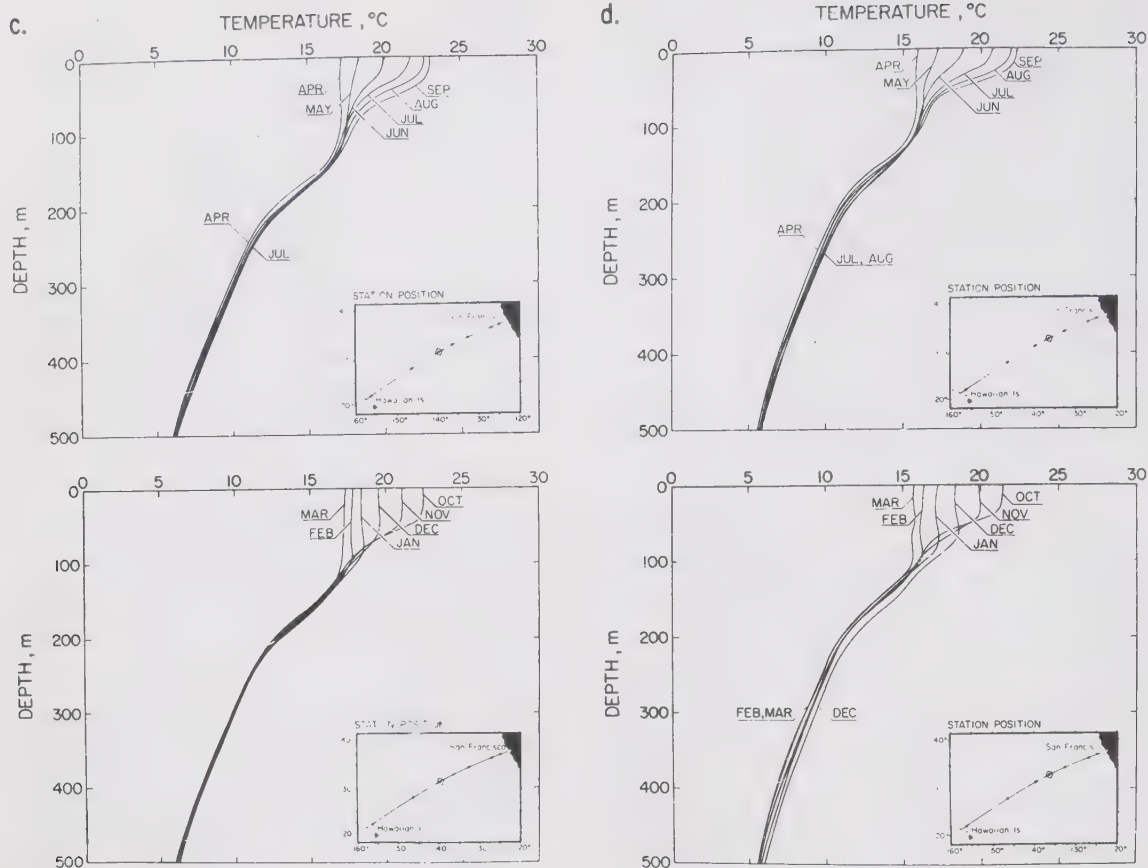


Figure 4.—Continued.

Coastal Upwelling

Reid et al. (1958) have described upwelling and the subsurface countercurrent along the California coast from repeated detailed oceanographic observations by the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program. Some effects of upwelling also appear in XBT mean temperatures, although sampling was poor at the California end of the route. In January, Appendix 1, the 9°C isotherm was closest to the surface (about 130 m) some 200 km from the California coast, but bent downward to 150 m at the coast. About late March the 9°C isotherm began to rise and reached a depth of about 120 m at the coast by mid-June, so that it then had nearly a uniform upward trend approaching the coast. Starting in September it began to sink again at the coast and the "ridge" in the isotherm again moved gradually offshore and by mid-November had returned to the position 200 km offshore where it was in January.

Coastal upwelling causes a delay in the onset of summer warming and a reduced range of the seasonally varying mean temperature. In the inshore area of the California Current (Fig. 3g), after a nearly constant winter temperature of about 12°C, summer warming at the sur-

face did not begin until late May or early June, as compared with April or May farther offshore (Fig. 3e, f). Also, in the inshore area the September temperature maximum reached only 16°C, for an annual range of only 4°C, whereas farther offshore (Fig. 3f) it reached 17.5°C for an annual range exceeding 5°C.

California Subsurface Countercurrent

In the vertical sections of Appendix 1 the downwarping of the 6°, 7°, and 8°C isotherms from 200 km at sea to the California coast shows warmer water against the coast (at depths of 200 to 500 m) than offshore. This agrees with observations of Reid et al. (1958) who reported the existence of a narrow northward moving undercurrent against the California coast and below 200 m. An exception occurred during April and May when the 8°C isotherm rose to about 200 m at the coast. This indicates that upwelling normally reached to that depth during these months. Another exception was the nearly level approach to the coast of the 8°C isotherm from mid-August to mid-September. This may reflect a brief late-summer upwelling period, but might just be the result of inadequate sampling immediately adjacent to the coast.

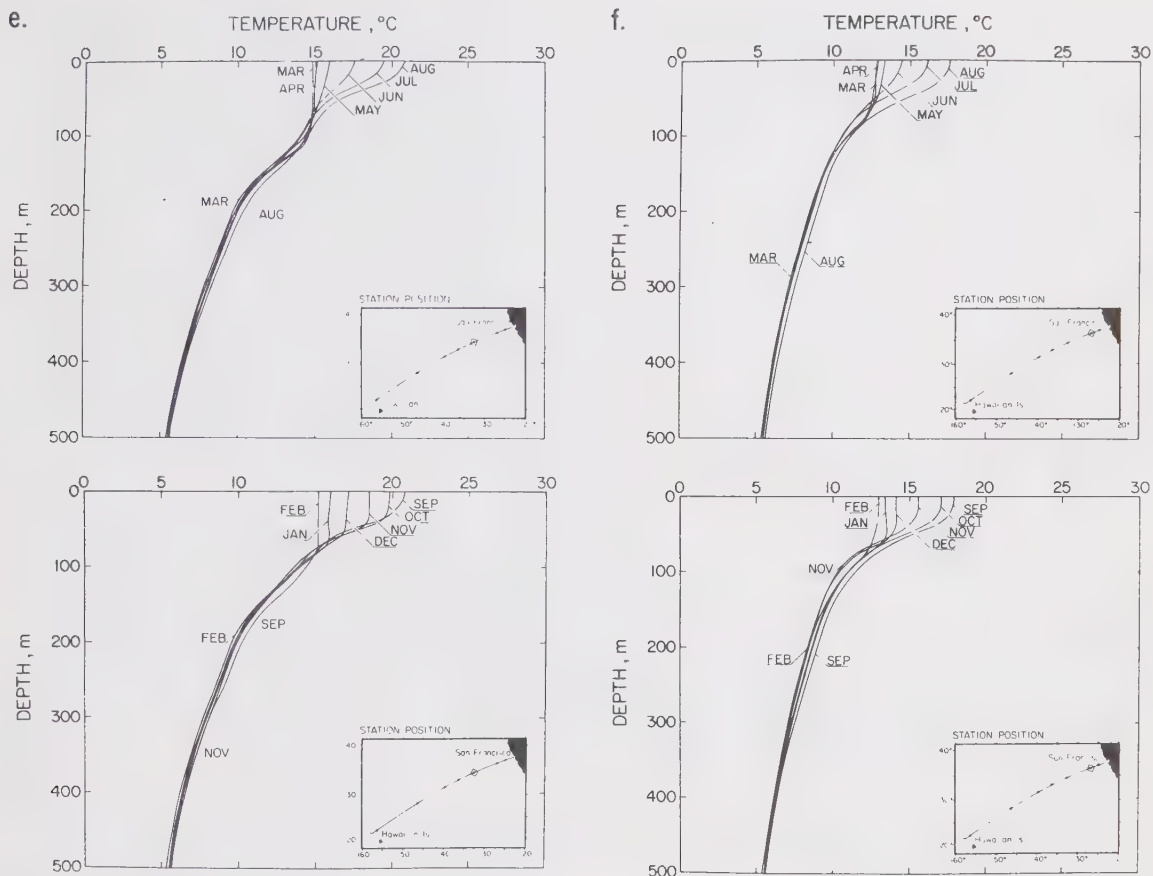


Figure 4.—Continued.

The 30-Day Temperature Changes

The lower panels of the figures in Appendix 1 show contours of temperature change in the upper 200 m during 30-day periods (of a 360-day yr). The maximum rate of warming was $2^{\circ}\text{C}/\text{mo}$ in June at the surface near 2,600 km, which is in the Transition Zone. The maximum rate of cooling was just over $1.5^{\circ}\text{C}/\text{mo}$ during November and December in the same area. The rate of cooling was smaller because the cooling takes place over a depth of at least 50 m whereas the warming is confined to a shallower layer of about 25 m. There was very little temperature change at any depth throughout the section from mid-March to mid-April, but there was no corresponding period in the fall.

In the fall period the downward mixing of heat into the upper thermocline as the surface cools is evident over most of the route in the temperature changes (Appendix 1) and in the vertical profiles (Fig. 4a-g). Beginning in August a subsurface maximum of warming appeared just above 50 m throughout most of the section. The level of maximum warming moved downward during the fall reaching 100 m in December. During this time the surface was cooling and a strong gradient of temperature change developed between the surface cooling and the

subsurface warming. The maximum subsurface warming decreased as its depth increased with time, and subsurface warming essentially disappeared by February.

The patterns of temperature change in the California Current region differ from those over most of the section. For example, from September through November and at distances of 3,200 to 3,400 km along the route, cooling extended downward from the surface to 200 m, at least. This created a break in the pattern of the warming maximum at 50 m, which existed over the rest of the section. A secondary center of cooling below 100 m occurred at 2,700 to 2,900 km on the route. These changes were associated with the development of a wave pattern in the isotherms along the permanent thermocline. The centers of cooling were associated with a steepening of the slope of the isotherms in the corresponding vertical sections, whereas in between these centers the isotherms flatten out. The steepening and flattening indicate a splitting of the broad flow of the California Current into filaments of stronger and weaker flow, respectively. The cooling pattern propagated westward along the section at a speed of about 100 km/mo (3.8 cm/s).

There was a counterpart center of warming which appeared in mid-December in the California Current region (around 3,400 km and 90 m) and which could be followed

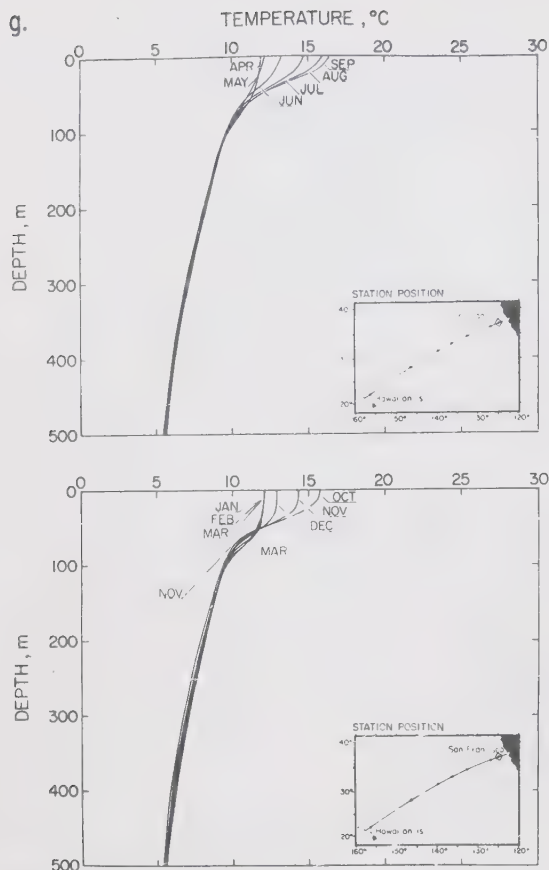


Figure 4.—Continued.

through early April propagating westward, also at the rate of 100 km/mo. This warming, however, was associated with the disappearance of the previously mentioned wave pattern along the thermocline.

From considerations of heat balance we may infer from the patterns of temperature changes that over most of the section vertical mixing dominates in transmitting the surface warming-cooling cycle downward to subsurface levels of 100 to 150 m. In contrast, horizontal advection of heat may be dominant in the California Current to depths of 200 to 300 m. The cause of the growth and decay of the wave pattern on the thermocline in the eastern part of the sections should be investigated.

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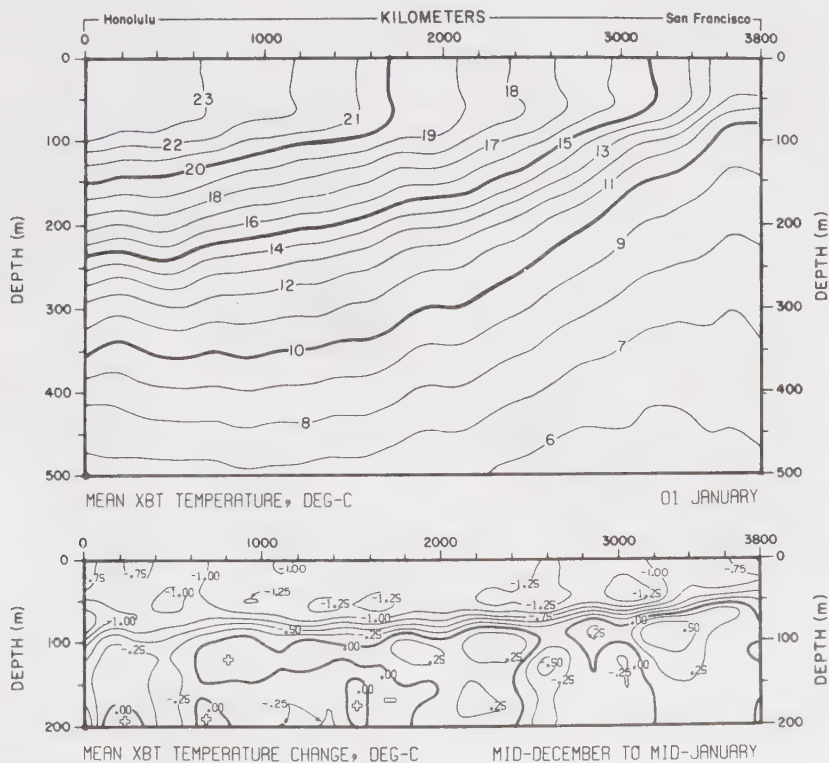
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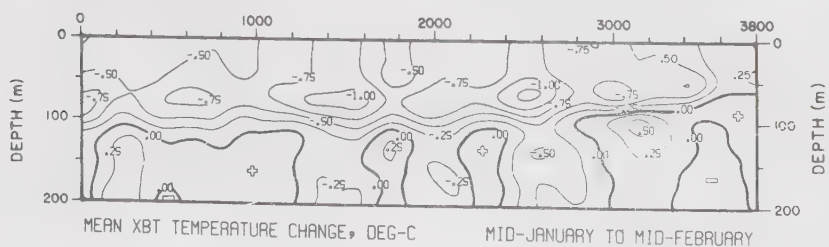
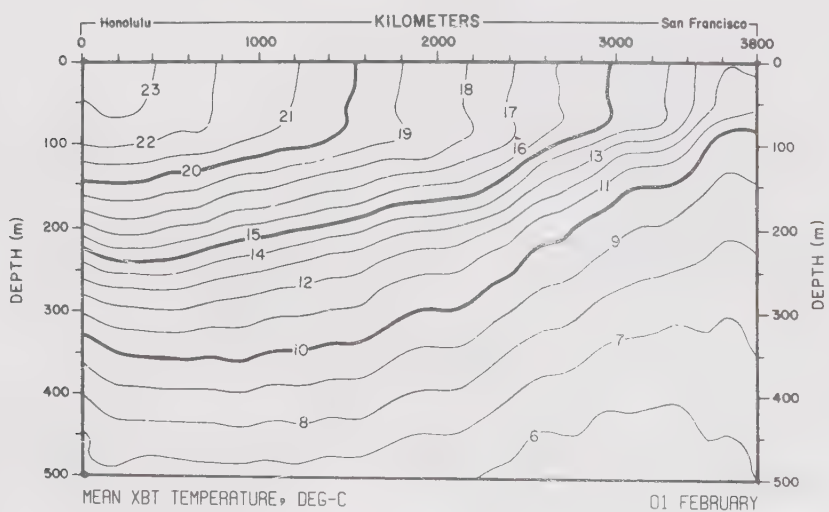
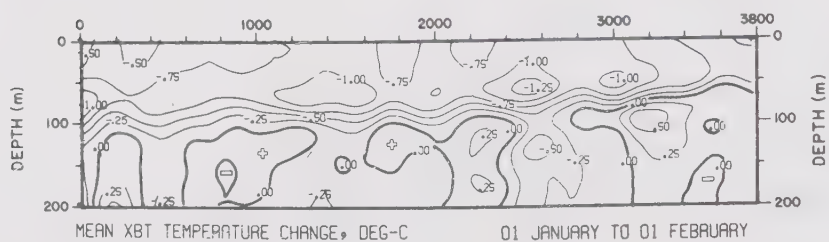
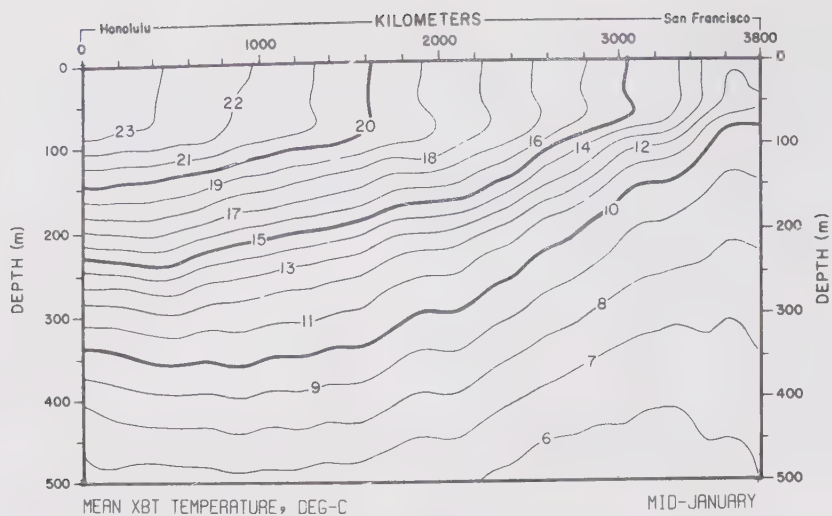
APPENDIX 1

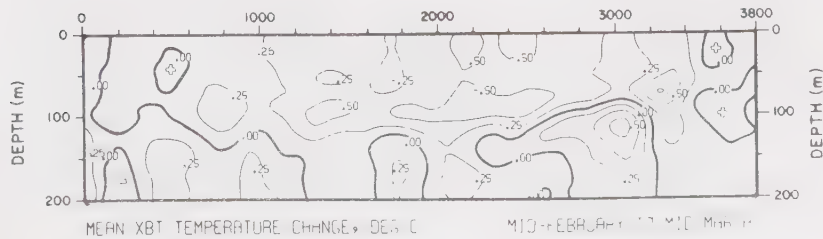
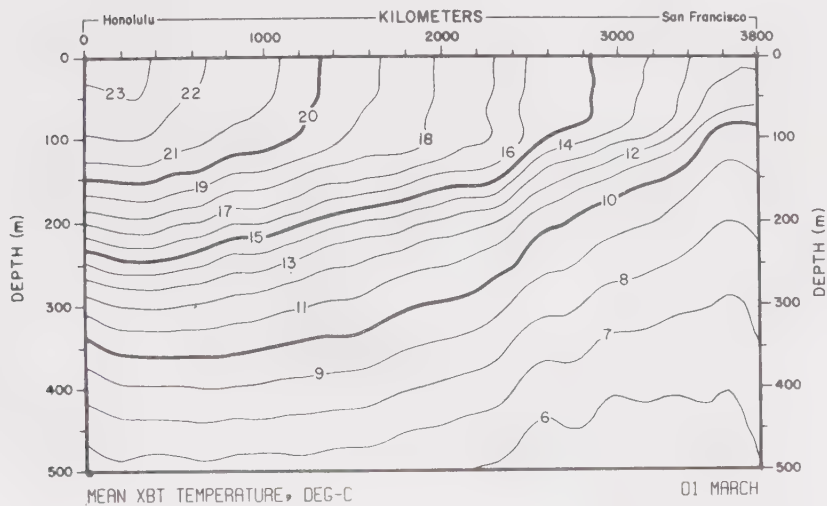
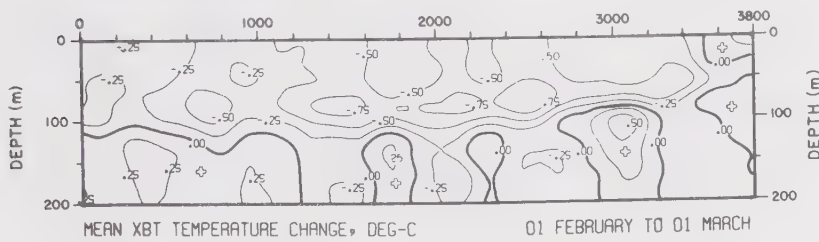
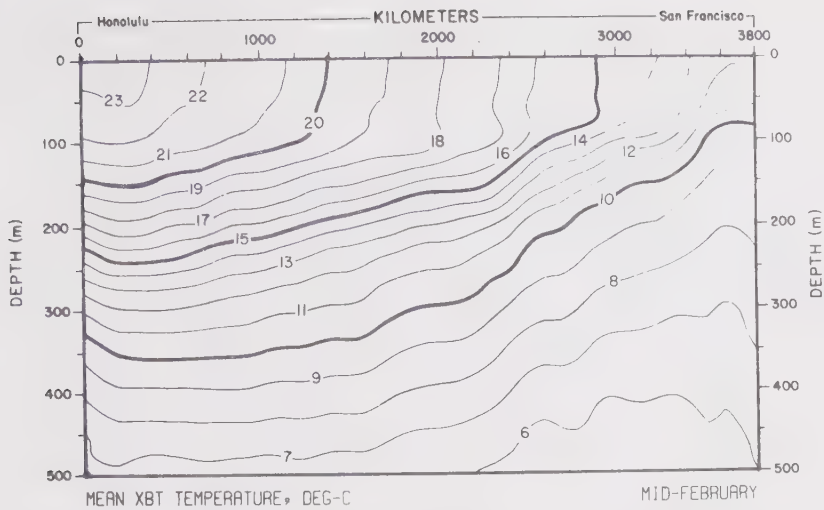
Vertical Sections of Mean Temperature and Mean "30-day" Temperature Change

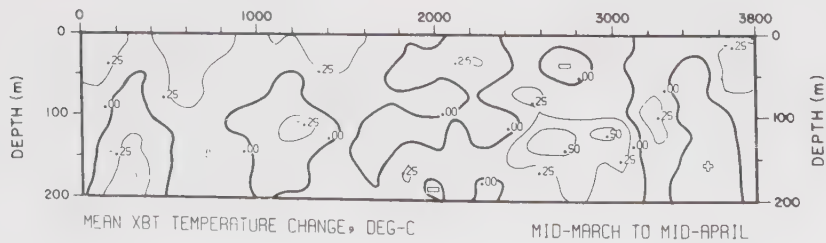
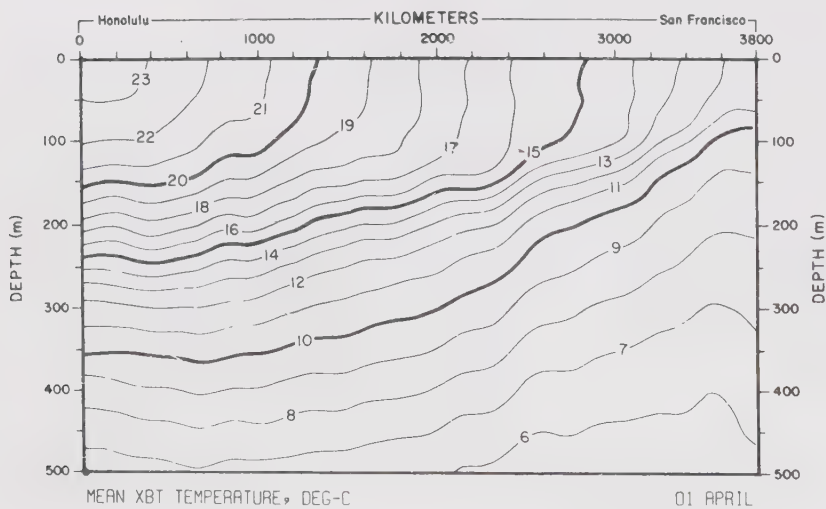
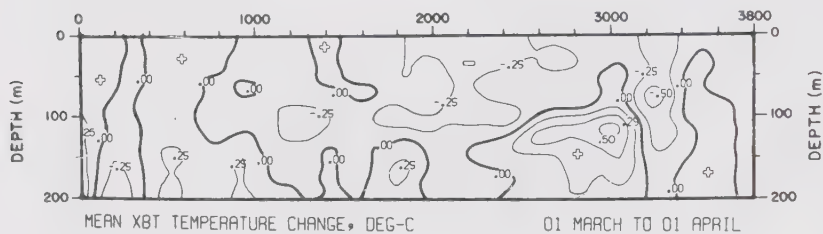
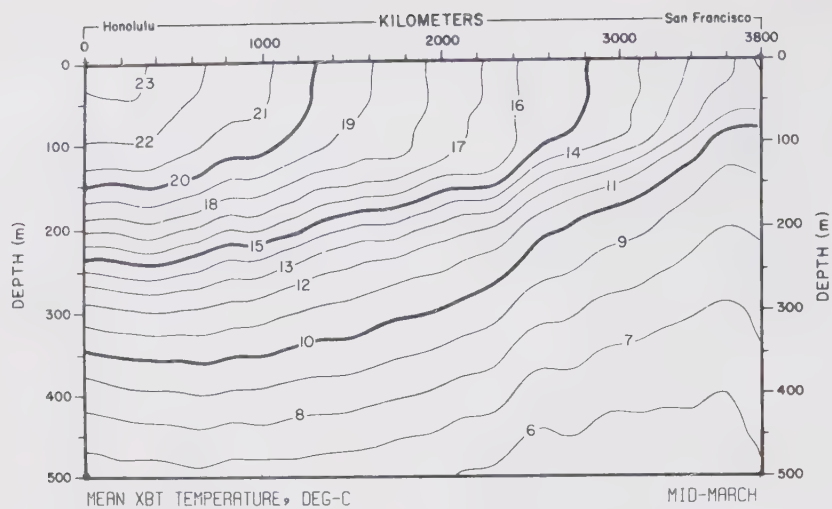
This Appendix contains 24 vertical sections of mean temperature ($^{\circ}\text{C}$), from the surface to 500 m, between San Francisco and Honolulu (upper panel) and spaced at 15-day intervals of a 360-day yr. The lower panel is a vertical section to 200 m showing the 30-day changes in temperature and centered on the date of the temperature section above it. For convenience the sections are labeled as: 01 January, mid-January, 01 February, etc., through mid-December.

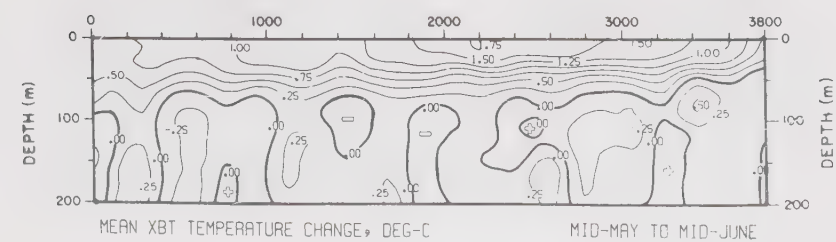
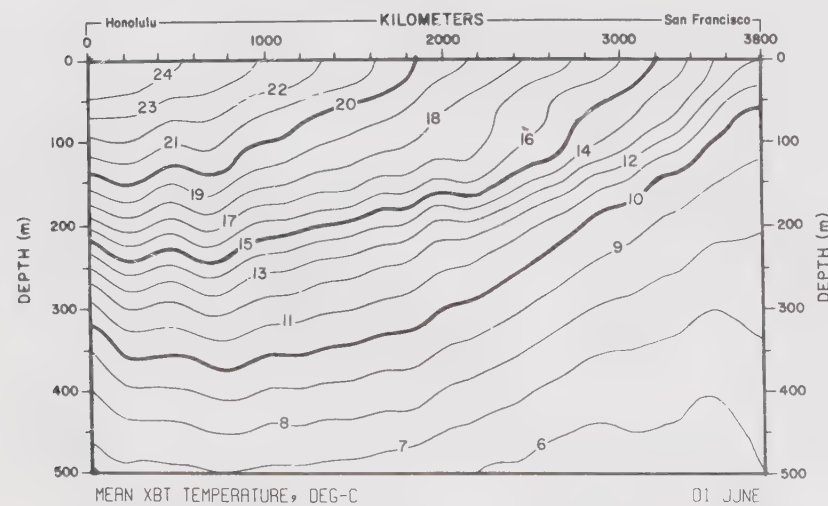
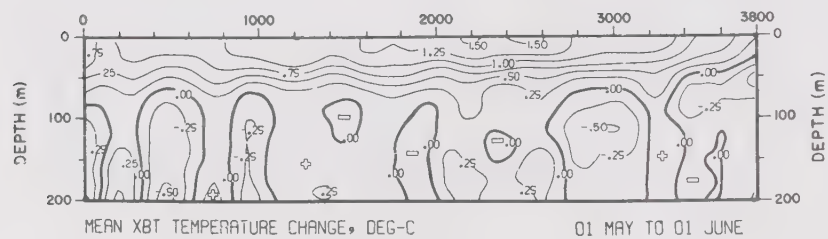
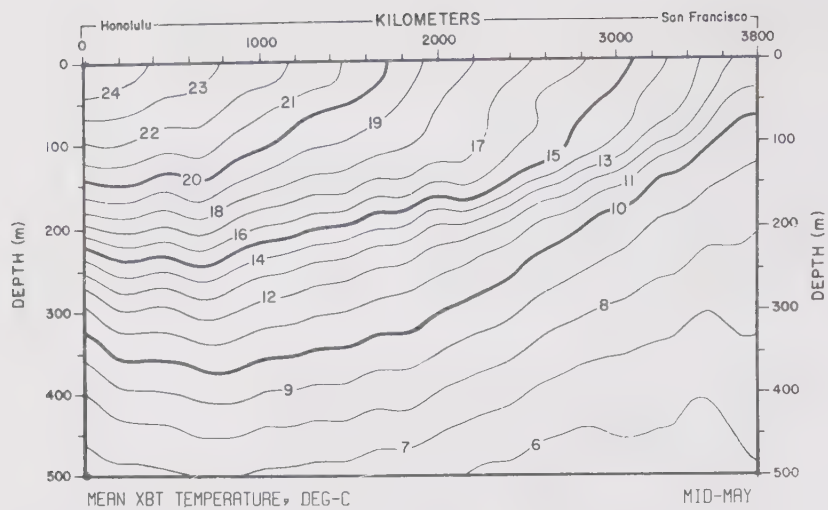
The grids of mean temperature were spatially smoothed, as explained in the text, before being contoured.

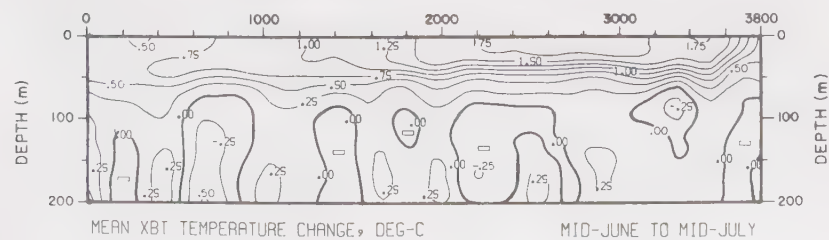
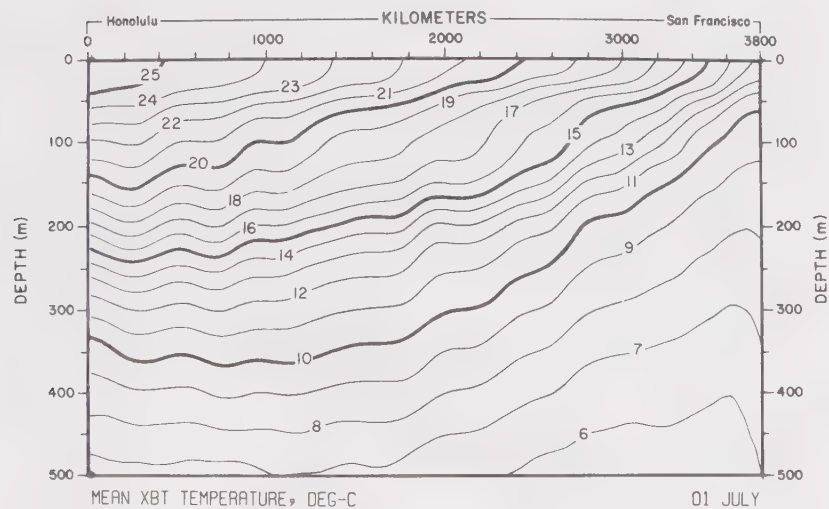
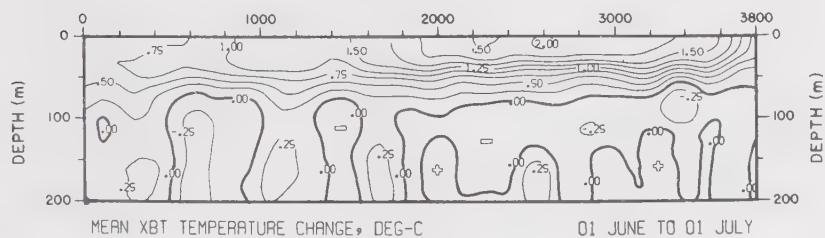
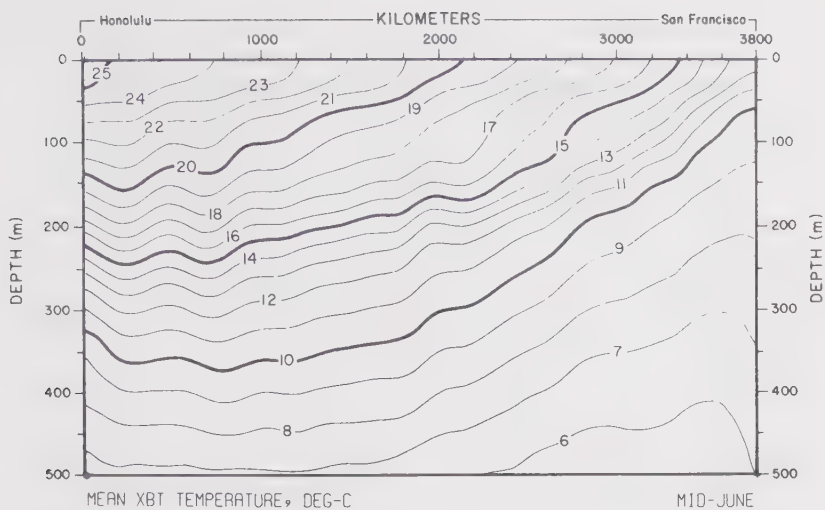


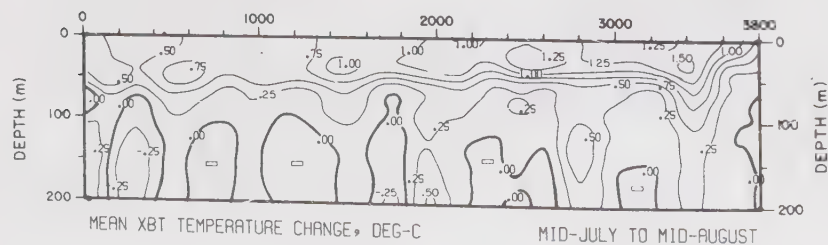
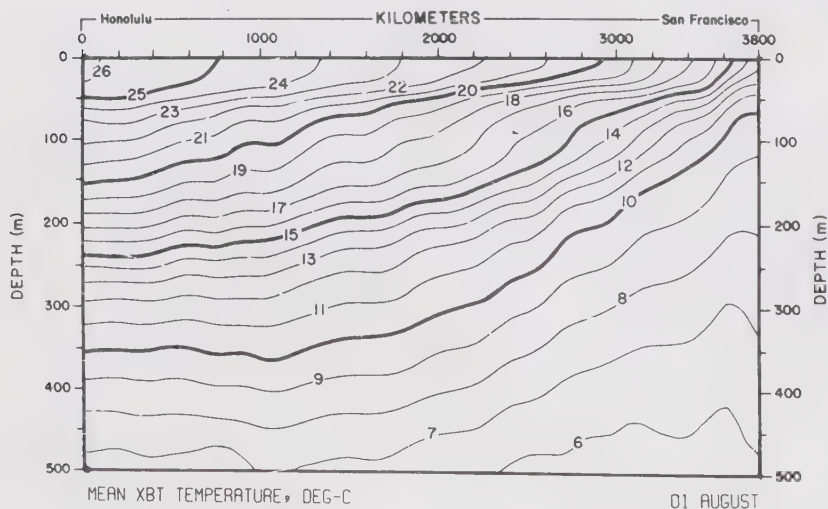
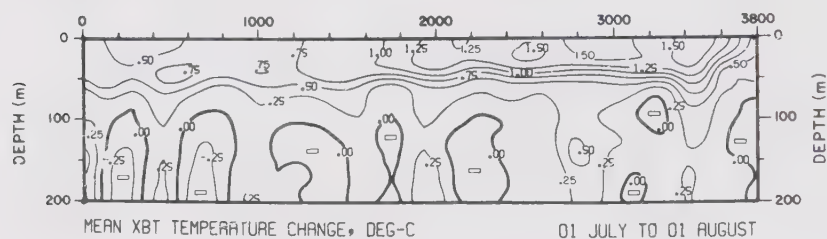
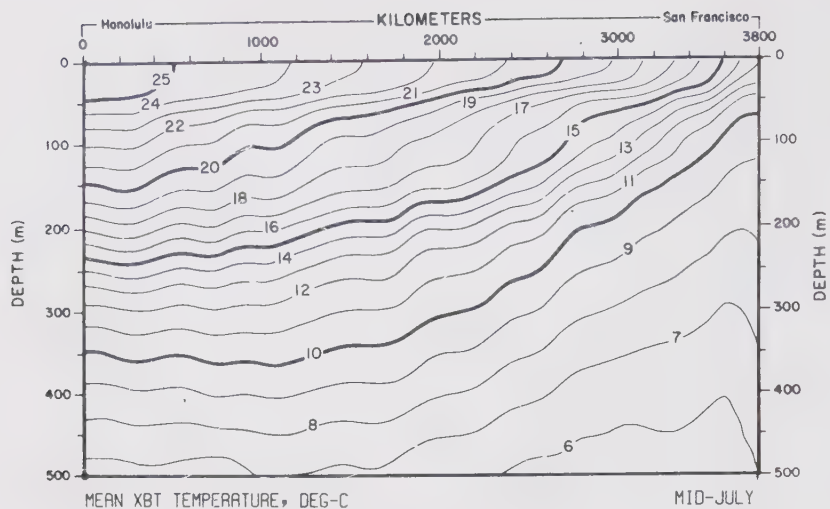


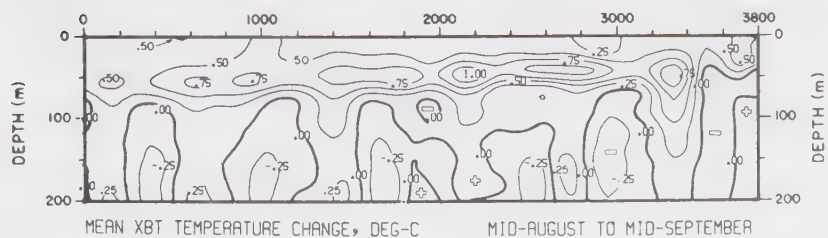
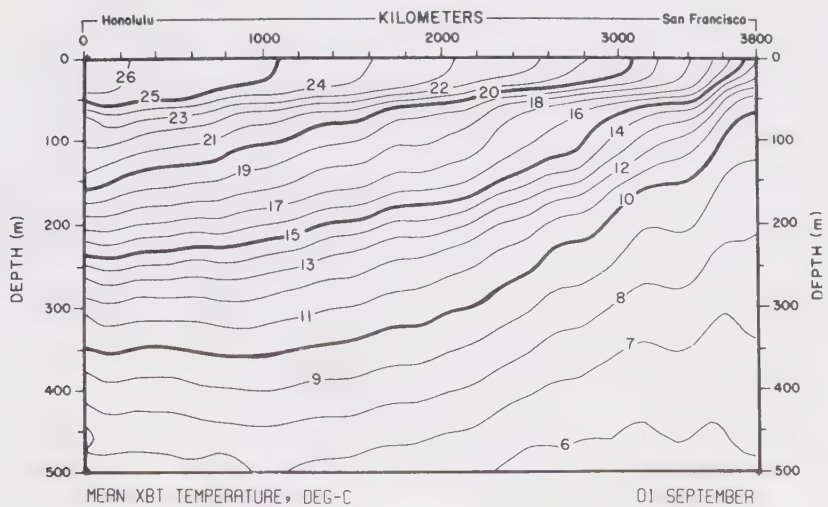
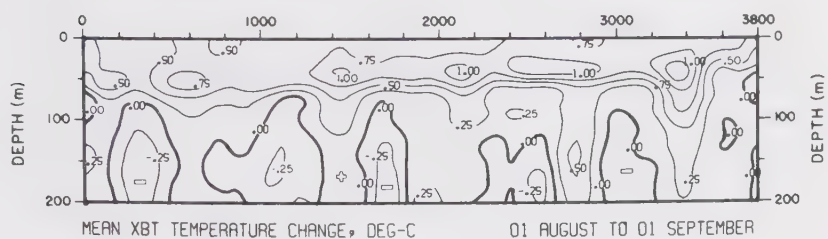
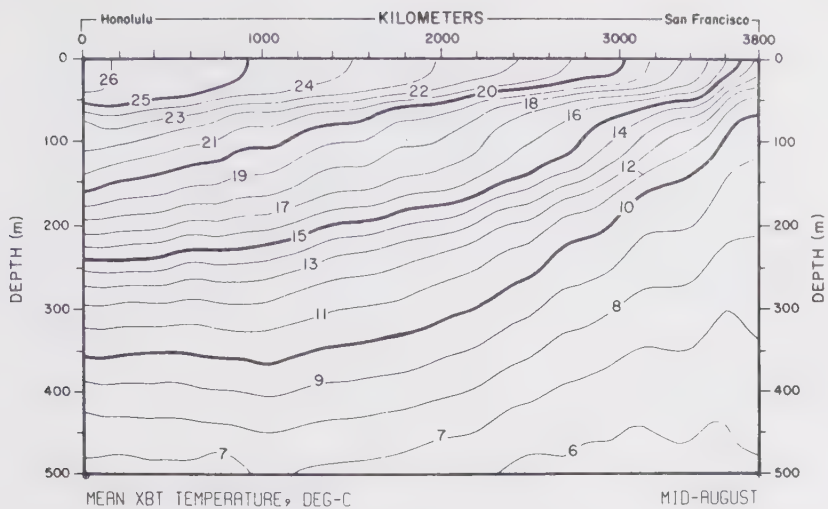


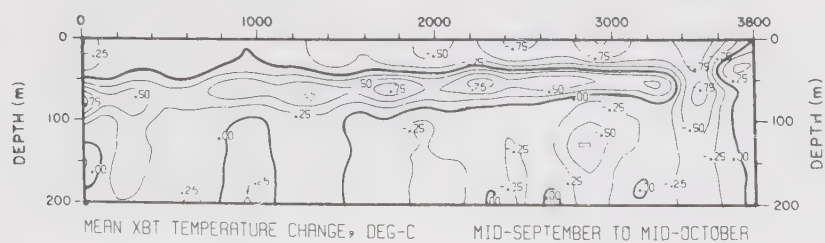
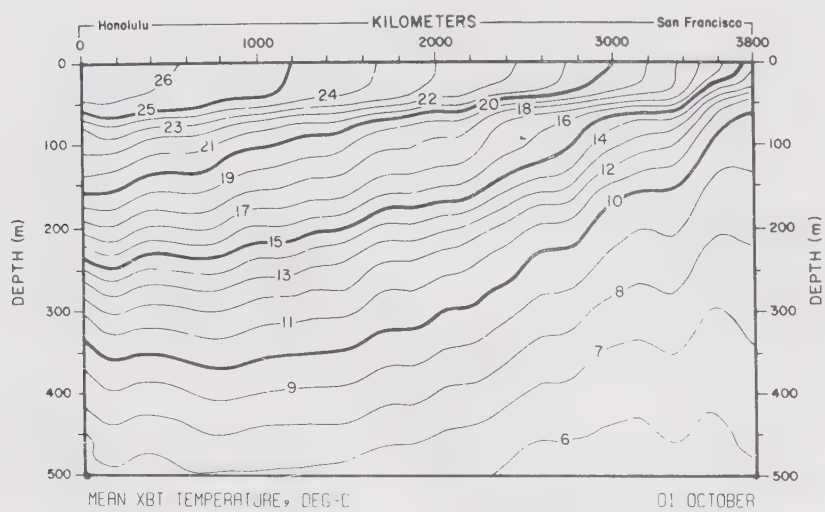
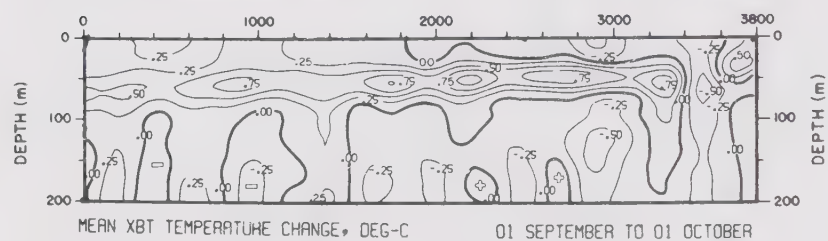
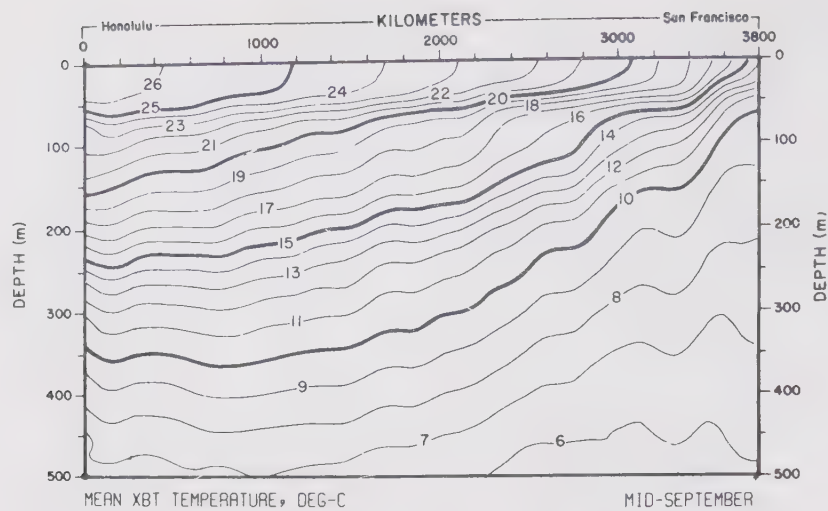


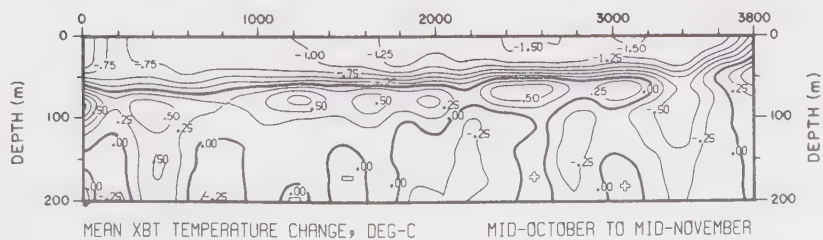
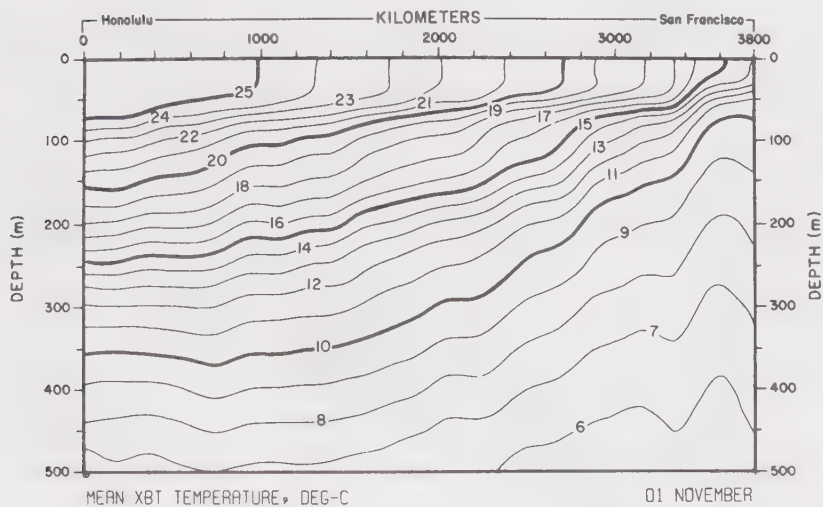
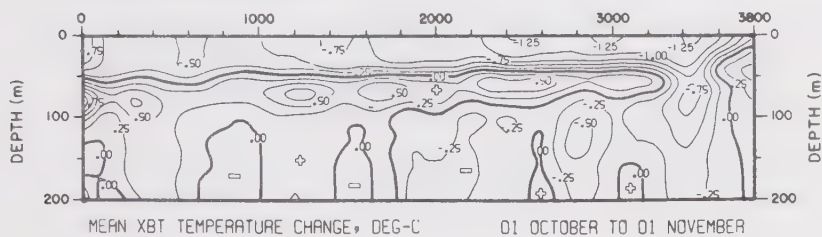
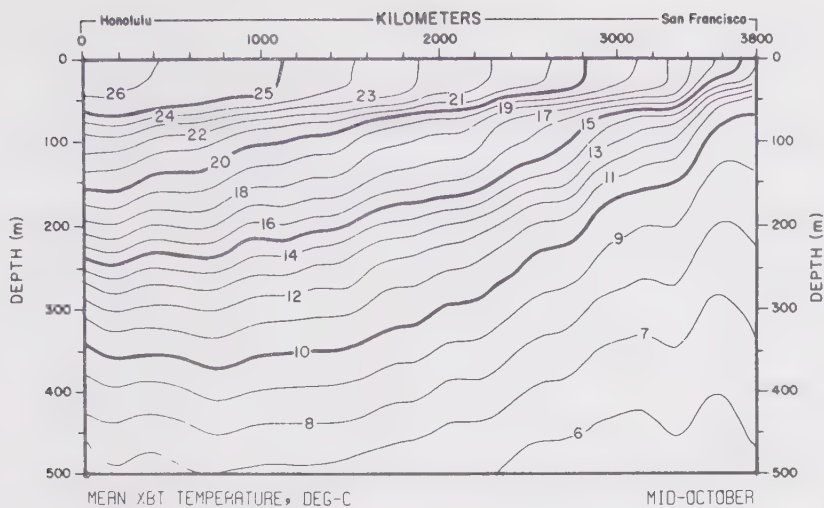


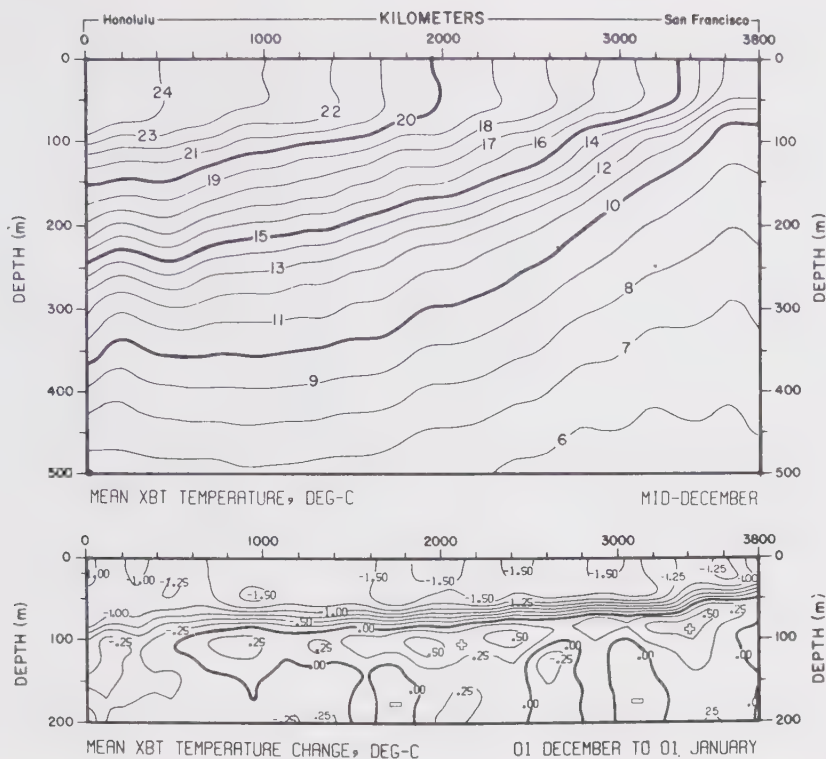












APPENDIX 2

Tables of Mean XBT Temperature

This Appendix contains 24 tables of mean temperatures ($^{\circ}\text{C}$) spaced at equal intervals throughout the year, corresponding to the temperature sections of Appendix 1. Each table contains, at alternating grid points, i.e., intervals of 185 km (100 n.mi.) on the San Francisco-Honolulu route, the mean temperature for selected depths, in meters. The mean temperatures are those computed from the fitted three-component harmonic function for the given distance and depth. These temperatures were abstracted from the complete grid, without smoothing.

MEAN XBT TEMPERATURE, DEG-C

01 JANUARY

0	23.9	23.9	23.2	23.0	22.6	22.3	21.8	21.4	20.9	19.8	19.3	18.9	18.2	17.7	16.7	16.4	15.5	14.9	13.7	12.3
10	23.9	23.8	23.2	23.0	22.6	22.3	21.8	21.4	20.8	19.8	19.3	18.9	18.2	17.6	16.7	16.3	15.5	14.9	13.8	12.3
20	23.9	23.8	23.2	23.1	22.5	22.3	21.8	21.4	20.8	19.7	19.3	18.9	18.2	17.6	16.7	16.3	15.5	15.0	13.8	12.2
30	23.9	23.8	23.2	23.1	22.5	22.3	21.8	21.4	20.8	19.7	19.3	18.9	18.1	17.6	16.8	16.2	15.5	15.0	13.8	12.2
40	23.9	23.8	23.2	23.1	22.5	22.2	21.8	21.3	20.8	19.7	19.3	18.9	18.1	17.7	16.9	16.1	15.6	15.0	13.9	12.1
50	24.0	23.8	23.2	23.1	22.5	22.2	21.8	21.4	20.9	19.7	19.3	19.0	18.3	17.8	17.0	16.3	15.7	15.0	13.9	11.9
D 60	24.0	23.7	23.2	23.1	22.5	22.2	21.9	21.4	20.9	19.8	19.4	19.0	18.4	17.9	17.1	16.2	15.7	14.8	13.5	11.4
E 70	24.0	23.7	23.2	23.1	22.4	22.1	21.9	21.4	21.0	19.8	19.5	18.9	18.3	17.8	16.8	15.7	15.4	14.5	12.8	10.6
P 80	23.8	23.4	23.1	22.9	22.1	21.8	21.6	21.1	20.7	19.6	19.4	18.8	18.0	17.5	16.4	15.4	14.4	13.7	11.9	10.0
T 90	23.3	22.9	22.8	22.5	21.6	21.4	21.0	20.7	20.2	19.2	19.2	18.4	17.6	17.0	15.7	14.5	13.3	12.7	11.3	9.7
H 100	22.8	22.4	22.3	22.0	21.1	20.8	20.3	20.1	19.7	18.8	18.8	17.9	17.2	16.4	15.0	13.9	12.6	12.0	11.0	9.5
120	21.5	21.1	21.1	20.6	20.1	19.7	19.1	18.9	18.6	17.5	17.9	17.1	16.2	15.3	14.2	13.0	11.7	11.0	10.1	9.1
(M) 150	20.0	19.6	19.7	19.2	18.6	18.2	17.7	17.4	17.0	16.2	16.2	15.8	14.7	13.9	12.8	11.6	10.4	9.9	9.4	8.8
200	17.2	17.2	17.4	16.5	16.1	15.8	15.2	15.0	14.5	13.4	13.2	12.9	12.0	11.3	10.5	9.9	9.2	9.0	8.6	8.1
250	13.9	14.1	14.7	13.6	13.4	13.2	12.7	12.5	12.3	11.6	11.1	11.0	10.4	10.0	9.4	9.0	8.4	8.1	7.9	7.5
300	11.4	11.5	11.9	11.6	11.6	11.5	11.2	11.1	10.9	10.5	9.9	9.9	9.4	9.0	8.4	8.0	7.6	7.4	7.2	7.0
400	8.4	8.6	8.8	8.9	8.9	8.9	8.8	8.6	8.6	8.3	7.8	7.8	7.4	7.1	6.7	6.5	6.4	6.2	6.2	6.2
500	6.7	6.6	6.6	6.6	6.8	6.8	6.7	6.5	6.6	6.4	6.2	6.3	5.9	5.7	5.5	5.6	5.5	5.5	5.6	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614
D I S T A N C E																				

MEAN XBT TEMPERATURE, DEG-C

MID-JANUARY

0	23.6	23.6	22.9	22.7	22.2	21.9	21.5	20.9	20.4	19.4	18.9	18.5	17.8	17.2	16.4	15.9	15.0	14.6	13.4	12.1
10	23.6	23.6	22.9	22.7	22.2	21.9	21.5	20.9	20.4	19.4	18.9	18.5	17.7	17.2	16.3	15.9	15.0	14.5	13.5	12.0
20	23.6	23.6	22.9	22.7	22.1	21.9	21.4	20.9	20.4	19.4	18.9	18.5	17.7	17.1	16.3	15.9	15.0	14.6	13.5	11.9
30	23.6	23.6	22.8	22.7	22.1	21.9	21.4	20.9	20.3	19.3	18.9	18.5	17.7	17.1	16.4	15.8	14.9	14.5	13.5	11.9
40	23.6	23.5	22.8	22.7	22.1	21.8	21.4	20.8	20.3	19.3	18.8	18.5	17.6	17.1	16.5	15.7	15.0	14.5	13.6	11.9
50	23.5	23.5	22.8	22.7	22.0	21.8	21.4	20.8	20.3	19.3	18.9	18.5	17.7	17.2	16.5	15.8	15.1	14.6	13.6	11.8
D 60	23.5	23.4	22.8	22.7	22.0	21.7	21.4	20.8	20.4	19.4	19.0	18.6	17.8	17.3	16.6	15.9	15.2	14.5	13.4	11.5
E 70	23.5	23.3	22.8	22.7	22.0	21.7	21.4	20.9	20.4	19.4	19.1	18.6	17.9	17.3	16.6	15.7	15.1	14.5	12.8	10.8
P 80	23.3	23.0	22.7	22.6	21.9	21.6	21.2	20.8	20.3	19.4	19.1	18.6	17.9	17.3	16.3	15.5	14.3	13.9	12.1	10.1
T 90	23.1	22.6	22.4	22.3	21.6	21.3	20.9	20.5	20.0	19.3	19.0	18.4	17.7	17.0	15.7	14.7	13.3	13.0	11.5	9.8
H 100	22.6	22.2	22.1	21.9	21.2	20.8	20.3	20.0	19.5	19.0	18.8	18.0	17.3	16.4	15.0	14.0	12.5	12.3	11.1	9.6
120	21.4	21.1	21.0	20.7	20.2	19.8	19.2	18.9	18.6	17.7	18.0	17.1	16.2	15.1	14.0	13.0	11.5	11.1	10.3	9.2
(M) 150	20.0	19.7	19.5	19.3	18.6	18.2	17.7	17.3	17.1	16.2	16.2	15.9	14.8	13.7	12.7	11.5	10.2	10.0	9.5	8.8
200	17.3	17.4	17.2	16.7	16.1	15.8	15.2	14.9	14.5	13.4	13.3	12.9	12.0	11.1	10.5	9.8	9.1	9.0	8.6	8.1
250	14.1	14.3	14.6	13.8	13.5	13.2	12.7	12.4	12.3	11.5	11.1	11.0	10.4	9.9	9.4	8.9	8.4	8.2	7.9	7.6
300	11.5	11.7	11.9	11.7	11.6	11.4	11.2	11.1	11.0	10.4	9.9	10.0	9.3	8.9	8.4	8.0	7.5	7.4	7.2	7.0
400	8.4	8.7	8.9	8.9	8.9	8.8	8.8	8.6	8.7	8.2	7.9	7.9	7.3	7.0	6.6	6.4	6.3	6.2	6.1	6.3
500	6.8	6.6	6.6	6.7	6.7	6.7	6.8	6.5	6.6	6.4	6.2	6.3	5.8	5.6	5.5	5.5	5.5	5.4	5.5	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614
D I S T A N C E																				

MEAN XBT TEMPERATURE, DEG-C

01 FEBRUARY

0	23.4	23.5	22.7	22.4	21.9	21.7	21.2	20.4	19.9	19.1	18.6	18.2	17.4	16.8	16.1	15.5	14.6	14.3	13.2	12.1
10	23.3	23.4	22.7	22.4	21.9	21.6	21.1	20.4	19.9	19.1	18.5	18.2	17.4	16.7	16.0	15.4	14.6	14.2	13.2	12.0
20	23.3	23.4	22.6	22.4	21.8	21.6	21.1	20.4	19.9	19.1	18.5	18.1	17.4	16.7	16.0	15.4	14.5	14.2	13.2	11.9
30	23.3	23.4	22.6	22.4	21.8	21.6	21.1	20.4	19.9	19.1	18.5	18.1	17.3	16.6	16.1	15.4	14.5	14.1	13.2	11.9
40	23.2	23.3	22.5	22.3	21.8	21.5	21.0	20.3	19.9	19.1	18.4	18.1	17.3	16.6	16.1	15.4	14.5	14.1	13.2	11.8
50	23.2	23.3	22.5	22.4	21.7	21.4	21.0	20.2	19.8	19.0	18.5	18.1	17.2	16.5	16.0	15.4	14.5	14.1	13.2	11.8
D 60	23.1	23.1	22.4	22.3	21.7	21.3	20.9	20.2	19.8	19.0	18.5	18.1	17.3	16.6	16.1	15.5	14.6	14.2	13.0	11.5
E 70	23.0	23.0	22.4	22.3	21.6	21.3	20.8	20.2	19.7	19.1	18.6	18.2	17.4	16.7	16.1	15.5	14.6	14.3	12.7	10.9
P 80	22.9	22.7	22.2	22.2	21.6	21.2	20.8	20.3	19.7	19.1	18.6	18.2	17.5	16.7	16.0	15.4	14.1	13.9	12.1	10.2
T 90	22.7	22.4	22.0	22.0	21.4	21.0	20.7	20.1	19.5	19.2	18.6	18.2	17.5	16.6	15.6	14.8	13.4	13.2	11.6	9.8
H 100	22.3	22.0	21.8	21.7	21.1	20.7	20.3	19.8	19.2	19.0	18.6	17.9	17.3	16.3	14.9	14.1	12.6	12.5	11.2	9.6
120	21.3	21.2	20.9	20.7	20.2	19.8	19.3	18.9	18.5	17.9	18.0	17.1	16.3	15.0	13.8	12.9	11.5	11.2	10.4	9.2
(M) 150	19.9	19.8	19.4	19.4	18.6	18.4	17.8	17.3	17.1	16.4	16.1	15.8	14.8	13.5	12.6	11.4	10.1	10.1	9.5	8.8
200	17.4	17.6	17.1	16.9	16.1	15.9	15.3	14.7	14.4	13.5	13.3	12.9	12.0	10.9	10.4	9.7	9.1	9.0	8.6	8.1
250	14.3	14.5	14.6	14.0	13.5	13.2	12.8	12.4	12.2	11.5	11.1	11.1	10.4	9.7	9.3	8.8	8.3	8.2	7.9	7.6
300	11.7	11.9	12.0	11.8	11.6	11.4	11.3	11.0	11.0	10.3	9.9	10.0	9.3	8.8	8.3	7.8	7.5	7.4	7.2	7.0
400	8.6	8.8	8.9	8.9	9.0	8.8	8.8	8.6	8.7	8.2	7.9	7.9	7.3	6.8	6.6	6.2	6.2	6.1	6.2	6.2
500	6.9	6.6	6.6	6.7	6.6	6.6	6.7	6.5	6.6	6.4	6.1	6.2	5.9	5.5	5.4	5.4	5.4	5.3	5.4	5.6
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614
D I S T A N C E																				

MEAN XBT TEMPERATURE, DEG-C

MID-FEBRUARY

0	23.3	23.3	22.7	22.3	21.7	21.5	20.9	20.0	19.6	19.0	18.3	17.9	17.2	16.4	15.8	15.1	14.3	14.0	13.1	12.1
10	23.2	23.3	22.6	22.3	21.7	21.5	20.9	20.0	19.6	19.0	18.3	17.9	17.2	16.3	15.8	15.1	14.3	13.9	13.1	12.1
20	23.2	23.3	22.6	22.2	21.7	21.4	20.9	20.0	19.6	19.0	18.3	17.9	17.1	16.3	15.8	15.1	14.3	13.9	13.0	12.1
30	23.1	23.3	22.5	22.2	21.6	21.4	20.8	20.0	19.6	18.9	18.2	17.8	17.2	16.2	15.8	15.2	14.3	13.8	13.0	12.0
40	23.1	23.2	22.4	22.1	21.6	21.3	20.8	19.9	19.5	18.9	18.2	17.8	17.1	16.2	15.8	15.2	14.2	13.8	12.9	11.8
50	23.0	23.2	22.3	22.1	21.5	21.2	20.7	19.9	19.5	19.0	18.2	17.7	17.0	16.1	15.7	15.1	14.2	13.7	12.7	11.7
D 60	22.8	23.0	22.2	22.0	21.4	21.1	20.6	19.8	19.3	18.9	18.2	17.7	16.9	16.0	15.7	15.2	14.2	13.9	12.6	11.5
E 70	22.7	22.8	22.1	21.9	21.3	21.0	20.5	19.8	19.2	18.8	18.2	17.7	17.0	16.1	15.7	15.3	14.2	13.9	12.4	11.0
P 80	22.6	22.6	22.0	21.9	21.3	21.0	20.4	19.8	19.2	18.8	18.2	17.8	17.2	16.2	15.7	15.2	13.9	13.7	12.0	10.3
T 90	22.4	22.3	21.8	21.8	21.2	20.8	20.4	19.7	19.1	18.9	18.2	17.8	17.2	16.2	15.4	14.8	13.5	13.1	11.6	9.9
H 100	22.1	22.0	21.6	21.5	20.9	20.6	20.1	19.5	18.9	18.9	18.3	17.6	17.1	16.0	14.9	14.1	12.8	12.5	11.1	9.6
120	21.3	21.3	20.9	20.7	20.2	19.9	19.4	18.8	18.3	18.1	17.9	16.9	16.4	14.9	13.6	12.9	11.6	11.3	10.4	9.2
(M) 150	19.9	20.0	19.5	19.5	18.6	18.5	17.9	17.3	17.0	16.6	16.0	15.7	14.9	13.3	12.3	11.3	10.2	10.1	9.4	8.8
200	17.5	17.7	17.1	17.1	16.1	16.0	15.4	14.6	14.2	13.7	13.2	12.7	12.1	10.7	10.3	9.6	9.2	9.0	8.5	8.1
250	14.5	14.7	14.6	14.2	13.4	13.3	12.9	12.3	12.1	11.5	11.1	11.0	10.5	9.6	9.2	8.7	8.3	8.2	7.8	7.5
300	11.9	12.1	12.1	11.9	11.6	11.4	11.3	11.0	10.9	10.3	10.0	9.9	9.3	8.6	8.3	7.7	7.5	7.4	7.2	7.0
400	8.6	8.9	8.9	9.0	9.0	8.8	8.8	8.6	8.6	8.1	7.9	7.8	7.3	6.7	6.6	6.2	6.2	6.1	6.2	6.1
500	6.8	6.7	6.7	6.8	6.5	6.5	6.7	6.6	6.6	6.4	6.1	6.1	5.9	5.5	5.5	5.3	5.4	5.3	5.4	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614
D I S T A N C E																				

MEAN XBT TEMPERATURE, DEG-C

01 MARCH

0	23.3	23.2	22.6	22.2	21.6	21.3	20.7	19.8	19.3	18.8	18.1	17.6	17.0	16.0	15.6	14.9	14.2	13.8	13.0	12.2
10	23.2	23.2	22.6	22.2	21.6	21.3	20.7	19.7	19.3	18.8	18.1	17.6	17.0	15.9	15.5	14.9	14.1	13.7	12.9	12.2
20	23.1	23.2	22.6	22.1	21.6	21.3	20.6	19.7	19.3	18.8	18.1	17.6	16.9	15.9	15.6	14.9	14.1	13.6	12.9	12.2
30	23.1	23.2	22.5	22.1	21.5	21.2	20.6	19.7	19.3	18.8	18.1	17.5	17.0	15.9	15.6	15.0	14.2	13.6	12.8	12.1
40	23.0	23.1	22.4	22.0	21.5	21.2	20.6	19.7	19.3	18.8	18.1	17.5	17.0	15.9	15.5	15.0	14.1	13.6	12.7	11.9
50	22.9	23.1	22.3	21.9	21.4	21.1	20.6	19.7	19.2	18.9	18.1	17.4	16.9	15.8	15.4	15.0	14.1	13.5	12.5	11.7
D 60	22.7	22.9	22.2	21.8	21.3	21.0	20.4	19.6	19.1	18.8	18.0	17.4	16.8	15.7	15.3	14.9	14.0	13.5	12.3	11.4
E 70	22.6	22.8	22.1	21.7	21.1	20.9	20.3	19.5	18.9	18.6	17.9	17.3	16.8	15.7	15.4	15.0	14.0	13.5	12.2	11.0
P 80	22.4	22.6	21.9	21.7	21.0	20.8	20.2	19.4	18.8	18.6	17.9	17.3	16.8	15.7	15.3	14.9	13.9	13.4	12.0	10.4
T 90	22.2	22.3	21.7	21.5	20.9	20.7	20.1	19.3	18.7	18.6	17.9	17.4	16.9	15.8	15.2	14.7	13.7	13.0	11.5	9.9
H 100	21.9	22.0	21.5	21.3	20.7	20.5	19.9	19.2	18.6	18.6	17.9	17.3	16.9	15.7	14.9	14.1	13.1	12.4	11.0	9.6
(M) 120	21.3	21.5	21.0	20.7	20.1	19.9	19.3	18.6	18.1	18.1	17.7	16.7	16.5	14.9	13.6	13.0	11.9	11.2	10.3	9.2
150	19.9	20.1	19.8	19.6	18.6	18.6	18.0	17.3	16.9	16.7	15.9	15.5	15.0	13.1	12.2	11.3	10.5	10.1	9.3	8.7
200	17.4	17.7	17.3	17.1	16.1	16.2	15.5	14.6	14.0	13.9	13.2	12.5	12.1	10.7	10.2	9.6	9.3	9.0	8.5	8.0
250	14.5	14.7	14.7	14.3	13.4	13.4	12.9	12.3	12.0	11.6	11.7	10.9	10.5	9.6	9.2	8.6	8.3	8.2	7.8	7.5
300	11.9	12.1	12.1	11.9	11.6	11.5	11.3	10.9	10.8	10.3	10.0	9.8	9.3	8.6	8.3	7.7	7.5	7.4	7.1	6.9
400	8.7	8.9	8.9	9.0	8.9	8.9	8.8	8.6	8.5	8.2	7.9	7.7	7.4	6.7	6.6	6.2	6.2	6.1	6.2	6.1
500	6.7	6.7	6.7	6.8	6.5	6.6	6.6	6.5	6.5	6.3	6.1	6.0	6.0	5.5	5.6	5.3	5.4	5.3	5.4	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KH	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

MID-MARCH

0	23.4	23.2	22.7	22.2	21.6	21.2	20.5	19.7	19.1	18.7	17.9	17.3	16.8	15.8	15.4	14.8	14.1	13.5	12.9	12.2
10	23.3	23.1	22.6	22.1	21.6	21.2	20.5	19.7	19.1	18.7	17.9	17.3	16.8	15.7	15.3	14.8	14.1	13.5	12.8	12.2
20	23.2	23.1	22.6	22.1	21.5	21.1	20.5	19.6	19.1	18.7	17.9	17.2	16.7	15.7	15.3	14.8	14.1	13.4	12.7	12.2
30	23.2	23.1	22.6	22.1	21.5	21.1	20.4	19.6	19.1	18.7	17.9	17.2	16.8	15.7	15.3	14.8	14.2	13.4	12.7	12.1
40	23.1	23.1	22.5	22.0	21.4	21.1	20.4	19.6	19.1	18.7	18.0	17.2	16.8	15.7	15.3	14.8	14.2	13.4	12.6	11.9
50	23.0	23.0	22.4	21.9	21.4	21.1	20.4	19.6	19.1	18.8	18.0	17.2	16.8	15.7	15.2	14.8	14.1	13.3	12.4	11.6
D 60	22.8	22.9	22.3	21.8	21.2	21.0	20.3	19.6	19.0	18.7	17.9	17.1	16.8	15.6	15.2	14.8	14.0	13.2	12.3	11.3
E 70	22.6	22.7	22.1	21.7	21.0	20.8	20.2	19.4	18.8	18.5	17.8	17.1	16.7	15.5	15.2	14.8	14.0	13.1	12.2	11.0
P 80	22.4	22.6	21.9	21.6	20.9	20.7	20.1	19.2	18.7	18.4	17.8	17.1	16.6	15.5	15.1	14.8	14.0	13.0	12.0	10.5
T 90	22.1	22.3	21.8	21.4	20.7	20.6	19.9	19.1	18.6	18.3	17.7	17.0	16.7	15.5	15.1	14.7	13.9	12.7	11.6	10.0
H 100	21.9	21.9	21.6	21.2	20.5	20.4	19.7	19.0	18.4	18.3	17.7	17.0	16.7	15.5	14.9	14.3	13.5	12.2	11.0	9.6
120	21.3	21.5	21.1	20.8	19.9	19.8	19.1	18.5	18.0	18.0	17.5	16.6	16.5	14.9	13.9	13.3	12.4	11.0	10.2	9.2
(M) 150	20.0	20.1	20.0	19.6	18.6	18.6	18.0	17.3	16.8	16.8	15.9	15.5	15.1	13.2	12.1	11.5	10.8	10.0	9.3	8.7
200	17.3	17.6	17.5	17.2	16.1	16.3	15.6	14.6	13.9	14.0	13.2	12.4	12.1	10.8	10.2	9.6	9.4	8.9	8.5	8.1
250	14.4	14.7	14.8	14.3	13.4	13.5	12.9	12.2	11.8	11.7	11.3	10.8	10.5	9.6	9.2	8.7	8.4	8.1	7.8	7.5
300	11.8	12.0	12.1	12.0	11.7	11.5	11.2	10.9	10.7	10.3	10.1	9.7	9.4	8.6	8.3	7.8	7.6	7.3	7.1	6.9
400	8.7	8.9	8.9	9.1	8.9	8.9	8.7	8.6	8.4	8.2	7.9	7.6	7.5	6.7	6.6	6.3	6.2	6.2	6.2	6.0
500	6.6	6.6	6.7	6.9	6.6	6.6	6.6	6.5	6.5	6.3	6.2	5.9	5.9	5.6	5.7	5.3	5.4	5.3	5.5	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KH	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

01 APRIL

0	23.5	23.2	22.8	22.3	21.7	21.2	20.5	19.9	19.1	18.7	17.8	17.1	16.7	15.7	15.3	14.9	14.2	13.4	12.8	12.1
10	23.5	23.2	22.7	22.2	21.6	21.2	20.5	19.8	19.1	18.7	17.8	17.1	16.6	15.6	15.3	14.8	14.1	13.3	12.7	12.1
20	23.4	23.2	22.7	22.2	21.6	21.1	20.4	19.8	19.1	18.7	17.8	17.1	16.6	15.6	15.2	14.8	14.2	13.3	12.7	12.0
30	23.3	23.1	22.7	22.2	21.5	21.1	20.3	19.7	19.1	18.7	17.8	17.1	16.6	15.7	15.2	14.8	14.2	13.3	12.7	12.0
40	23.2	23.1	22.6	22.1	21.4	21.1	20.3	19.7	19.1	18.7	17.9	17.1	16.7	15.7	15.2	14.8	14.2	13.3	12.6	11.8
50	23.1	23.0	22.5	22.0	21.4	21.0	20.3	19.7	19.1	18.7	17.9	17.1	16.8	15.7	15.2	14.8	14.2	13.2	12.5	11.5
D 60	22.9	22.8	22.4	21.9	21.2	21.0	20.2	19.6	19.0	18.6	17.9	17.1	16.8	15.6	15.2	14.8	14.1	13.0	12.4	11.2
E 70	22.8	22.7	22.2	21.8	21.0	20.8	20.2	19.4	18.9	18.5	17.9	17.0	16.7	15.6	15.2	14.7	14.1	12.9	12.3	10.9
P 80	22.5	22.5	22.0	21.7	20.9	20.7	20.0	19.2	18.8	18.3	17.8	17.0	16.6	15.5	15.1	14.7	14.1	12.7	12.1	10.5
T 90	22.2	22.2	21.8	21.5	20.7	20.5	19.7	19.1	18.6	18.2	17.7	17.0	16.6	15.5	15.1	14.7	14.1	12.5	11.7	10.0
H 100	21.9	21.9	21.6	21.3	20.5	20.3	19.5	18.9	18.4	18.1	17.6	16.9	16.6	15.4	15.1	14.5	13.8	12.0	11.1	9.6
120	21.4	21.4	21.1	20.8	19.9	19.7	18.9	18.4	17.9	17.9	17.4	16.7	16.5	15.0	14.2	13.6	12.8	10.9	10.2	9.2
(M) 150	20.0	20.0	20.0	19.7	18.7	18.6	18.0	17.3	16.8	16.8	15.9	15.6	15.2	13.3	12.2	11.7	11.1	9.8	9.3	8.8
200	17.2	17.5	17.6	17.2	16.2	16.3	15.6	14.6	13.9	14.0	13.2	12.4	12.1	10.9	10.2	9.8	9.4	8.8	8.5	8.1
250	14.2	14.6	14.8	14.4	13.5	13.4	12.9	12.2	11.8	11.7	11.3	10.8	10.6	9.7	9.2	8.8	8.5	8.1	7.8	7.5
300	11.7	11.9	12.1	12.1	11.7	11.6	11.2	10.9	10.6	10.4	10.1	9.6	9.5	8.6	8.3	7.9	7.7	7.3	7.1	7.0
400	8.6	8.8	8.9	9.2	8.9	8.9	8.7	8.6	8.3	8.2	8.0	7.5	7.5	6.8	6.6	6.5	6.4	6.2	6.2	6.1
500	6.5	6.6	6.7	6.9	6.7	6.7	6.6	6.5	6.4	6.3	6.2	5.9	5.9	5.6	5.7	5.4	5.5	5.4	5.5	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

MID-APRIL

0	23.7	23.4	23.0	22.5	21.9	21.4	20.6	20.2	19.4	18.9	17.9	17.2	16.7	15.9	15.5	15.0	14.3	13.4	12.8	12.0
10	23.7	23.4	22.9	22.4	21.9	21.4	20.6	20.2	19.3	18.8	17.9	17.1	16.7	15.8	15.3	14.9	14.3	13.4	12.7	11.9
20	23.6	23.3	22.9	22.4	21.8	21.3	20.5	20.1	19.3	18.8	17.9	17.1	16.6	15.8	15.2	14.9	14.3	13.3	12.7	11.8
30	23.6	23.2	22.8	22.4	21.7	21.2	20.4	20.1	19.2	18.8	17.8	17.1	16.6	15.8	15.2	14.8	14.3	13.3	12.7	11.8
40	23.4	23.2	22.7	22.3	21.6	21.1	20.3	20.0	19.2	18.7	17.9	17.1	16.6	15.8	15.2	14.8	14.3	13.3	12.7	11.6
50	23.3	23.0	22.6	22.2	21.5	21.0	20.2	19.9	19.2	18.6	17.9	17.2	16.7	15.8	15.2	14.9	14.3	13.2	12.7	11.3
D 60	23.1	22.8	22.4	22.0	21.3	21.0	20.2	19.7	19.1	18.6	17.9	17.2	16.8	15.8	15.3	14.8	14.3	13.0	12.6	11.1
E 70	22.9	22.6	22.3	22.0	21.1	20.9	20.1	19.5	19.1	18.5	17.9	17.2	16.8	15.8	15.3	14.8	14.2	12.8	12.4	10.8
P 80	22.6	22.4	22.1	21.8	21.0	20.7	19.9	19.3	18.9	18.3	17.9	17.1	16.7	15.7	15.2	14.8	14.2	12.7	12.1	10.5
T 90	22.3	22.1	21.9	21.6	20.7	20.5	19.7	19.2	18.7	18.1	17.8	17.1	16.6	15.7	15.2	14.7	14.1	12.4	11.7	10.0
H 100	22.1	21.8	21.6	21.4	20.5	20.3	19.4	18.9	18.5	18.0	17.6	17.0	16.6	15.5	15.2	14.6	13.9	11.9	11.1	9.7
120	21.4	21.2	20.9	20.9	19.8	19.6	18.7	18.4	17.9	17.7	17.3	16.8	16.4	15.2	14.5	13.9	13.0	10.7	10.1	9.2
(M) 150	19.9	19.9	19.6	19.8	18.7	18.4	17.9	17.3	16.8	16.7	15.9	15.8	15.2	13.5	12.5	11.8	11.2	9.7	9.4	8.8
200	17.1	17.3	17.5	17.2	16.3	16.2	15.6	14.7	14.0	14.0	13.2	12.6	12.1	11.0	10.3	9.9	9.5	8.8	8.6	8.2
250	14.1	14.5	14.6	14.5	13.7	13.3	12.9	12.3	11.8	11.7	11.4	10.8	10.5	9.8	9.3	9.0	8.6	8.1	7.9	7.6
300	11.5	11.8	11.9	12.2	11.8	11.5	11.2	10.9	10.6	10.4	10.2	9.7	9.5	8.8	8.3	8.0	7.8	7.3	7.2	7.1
400	8.5	8.8	8.9	9.2	9.0	8.9	8.7	8.6	8.3	8.2	8.0	7.6	7.5	6.9	6.6	6.6	6.5	6.3	6.2	6.2
500	6.6	6.7	6.8	7.0	6.8	6.7	6.6	6.5	6.4	6.3	6.2	5.9	5.8	5.6	5.7	5.5	5.6	5.5	5.5	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

01 MAY

0	24.0	23.7	23.3	22.4	22.1	21.4	21.1	20.7	19.9	19.2	18.3	17.6	17.1	16.4	15.9	15.4	14.7	13.7	12.9	12.0
10	24.0	23.7	23.2	22.4	22.1	21.7	21.0	20.7	19.8	19.2	18.2	17.5	17.0	16.3	15.7	15.3	14.6	13.6	12.9	11.9
20	23.9	23.7	23.2	22.7	22.2	21.7	20.9	20.7	19.8	19.2	18.2	17.4	16.9	16.2	15.6	15.2	14.6	13.5	12.9	11.7
30	23.9	23.5	23.0	22.6	22.0	21.5	20.8	20.5	19.7	19.1	18.0	17.4	16.8	16.1	15.4	15.0	14.4	13.4	12.8	11.6
40	23.7	23.4	22.8	22.5	21.8	21.3	20.6	20.3	19.5	19.0	18.0	17.4	16.8	16.0	15.4	15.0	14.4	13.4	12.9	11.4
50	23.5	23.1	22.6	22.4	21.6	21.1	20.4	20.1	19.4	18.8	18.0	17.4	16.8	16.0	15.4	15.0	14.3	13.3	12.8	11.2
D 60	23.2	22.8	22.5	22.3	21.5	21.0	20.2	19.8	19.3	18.7	18.0	17.4	16.8	16.0	15.4	14.9	14.3	13.1	12.7	10.9
E 70	23.0	22.6	22.2	22.1	21.3	20.8	20.1	19.6	19.2	18.6	18.0	17.4	16.9	16.0	15.5	14.9	14.3	13.0	12.4	10.7
P 80	22.7	22.3	22.0	21.9	21.1	20.6	19.9	19.5	19.1	18.4	18.0	17.4	16.8	16.0	15.4	14.8	14.2	12.7	12.1	10.4
1 90	22.4	22.1	21.8	21.8	20.8	20.4	19.6	19.3	18.8	18.2	17.9	17.3	16.7	15.9	15.3	14.7	14.0	12.4	11.7	10.0
II 100	22.1	21.8	21.4	21.5	20.5	20.2	19.3	19.0	18.5	18.1	17.7	17.2	16.7	15.7	15.3	14.6	13.9	11.8	11.1	9.7
120	21.4	21.1	20.7	20.9	19.9	19.5	18.7	18.4	18.0	17.7	17.2	17.0	16.4	15.3	14.7	13.9	12.9	10.7	10.1	9.3
(M) 150	19.9	19.8	19.5	19.8	18.8	18.3	17.8	17.4	16.8	16.7	15.9	16.0	15.3	13.7	12.8	11.8	11.2	9.7	9.4	8.9
200	17.1	17.3	17.2	17.4	16.4	15.9	15.0	14.8	14.2	14.0	13.1	12.8	12.1	11.1	10.5	9.9	9.5	8.7	8.6	8.3
250	14.0	14.4	14.4	14.7	13.9	13.3	12.9	12.5	12.0	11.8	11.4	10.9	10.5	9.8	9.4	9.0	8.7	8.1	7.9	7.6
300	11.4	11.8	11.8	12.3	11.9	11.5	11.3	11.0	10.7	10.5	10.2	9.8	9.5	8.9	8.4	8.1	7.8	7.4	7.2	7.2
400	8.4	8.8	8.9	9.2	9.1	8.9	8.6	8.6	8.3	8.3	8.1	7.6	7.4	7.0	6.6	6.6	6.5	6.3	6.1	6.3
500	6.6	6.7	6.8	7.0	7.0	6.8	6.7	6.6	6.4	6.3	6.2	5.9	5.8	5.6	5.6	5.5	5.7	5.6	5.4	5.6
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

MID-MAY

0	24.3	24.2	23.7	23.3	22.3	22.3	21.8	21.3	20.5	19.8	18.9	18.3	17.7	17.1	16.6	16.0	15.2	14.3	13.3	12.2
10	24.3	24.2	23.7	23.2	22.4	22.3	21.7	21.3	20.5	19.8	18.8	18.2	17.6	17.0	16.4	15.8	15.1	14.1	13.2	12.0
20	24.3	24.1	23.5	23.1	22.7	22.2	21.5	21.2	20.4	19.7	18.7	18.1	17.5	16.8	16.2	15.7	15.0	14.0	13.1	11.8
30	24.2	24.0	23.3	23.0	22.5	22.0	21.4	21.0	20.3	19.6	18.5	17.9	17.3	16.6	15.9	15.5	14.8	13.8	13.1	11.7
40	24.0	23.7	23.0	22.8	22.2	21.7	21.1	20.6	20.0	19.4	18.3	17.7	17.1	16.3	15.7	15.3	14.6	13.6	13.0	11.5
50	23.7	23.4	22.7	22.6	21.9	21.3	20.7	20.3	19.8	19.2	18.2	17.7	17.0	16.2	15.6	15.1	14.4	13.5	12.8	11.1
D 60	23.4	23.1	22.4	22.5	21.7	21.1	20.4	19.9	19.5	19.0	18.1	17.7	16.9	16.2	15.6	15.0	14.4	13.3	12.5	10.7
E 70	23.0	22.7	22.2	22.2	21.5	20.8	20.1	19.7	19.3	18.8	18.0	17.6	16.9	16.2	15.6	14.9	14.3	13.2	12.2	10.5
P 80	22.7	22.4	21.9	22.0	21.2	20.6	19.9	19.5	19.1	18.6	18.0	17.6	16.9	16.1	15.5	14.8	14.1	12.9	11.8	10.2
T 90	22.5	22.1	21.6	21.8	20.9	20.4	19.7	19.3	18.9	18.4	17.9	17.5	16.8	16.0	15.3	14.6	13.9	12.4	11.4	10.0
H 100	22.1	21.8	21.2	21.5	20.6	20.1	19.4	19.0	18.6	18.2	17.7	17.4	16.7	15.8	15.2	14.4	13.6	11.9	11.0	9.7
120	21.4	21.1	20.4	20.9	19.9	19.4	18.7	18.5	18.0	17.7	17.1	17.2	16.3	15.4	14.7	13.7	12.7	10.8	10.1	9.3
(M) 150	19.9	19.9	19.1	19.8	18.8	18.2	17.7	17.4	16.9	16.8	15.8	16.2	15.3	13.9	13.1	11.7	11.1	9.7	9.4	9.0
200	17.2	17.4	16.8	17.5	16.5	15.8	15.5	15.0	14.4	14.1	13.0	13.0	12.1	11.1	10.6	9.8	9.5	8.8	8.6	8.3
250	14.0	14.5	14.1	14.6	14.0	13.3	12.9	12.6	12.1	11.9	11.3	11.0	10.6	9.9	9.4	9.0	8.7	8.1	7.9	7.7
300	11.4	12.0	11.8	12.4	12.0	11.5	11.4	11.1	10.8	10.6	10.2	9.9	9.5	8.9	8.4	8.1	7.8	7.4	7.2	7.2
400	8.4	8.9	8.9	9.2	9.1	8.9	8.9	8.7	8.5	8.4	8.1	7.8	7.4	7.0	6.7	6.5	6.5	6.3	6.0	6.3
500	6.7	6.7	6.9	7.0	7.0	6.8	6.8	6.7	6.5	6.4	6.2	6.0	5.8	5.7	5.5	5.6	5.7	5.6	5.4	5.6
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

01 JUNE

	0	24.7	24.6	24.1	23.7	23.4	22.9	22.4	21.9	21.2	20.5	19.6	19.1	18.5	17.9	17.3	16.6	15.9	14.9	13.8	12.6
	10	24.6	24.6	24.1	23.6	23.3	22.8	22.3	21.8	21.1	20.4	19.5	19.0	18.4	17.8	17.1	16.5	15.8	14.8	13.6	12.4
	20	24.6	24.5	23.9	23.5	23.2	22.7	22.2	21.7	21.1	20.3	19.4	18.9	18.2	17.5	16.9	16.3	15.6	14.6	13.5	12.2
	30	24.5	24.3	23.6	23.3	22.9	22.5	22.0	21.5	20.9	20.1	19.1	18.5	17.9	17.1	16.5	16.0	15.3	14.2	13.4	12.0
	40	24.3	24.1	23.3	23.1	22.6	22.1	21.6	21.0	20.4	19.9	18.7	18.2	17.6	16.7	16.1	15.7	15.0	14.0	13.1	11.6
	50	23.9	23.7	22.9	22.8	22.3	21.6	21.1	20.5	20.1	19.6	18.6	18.0	17.3	16.5	15.9	15.3	14.6	13.8	12.7	11.1
D	60	23.5	23.3	22.5	22.5	21.9	21.2	20.6	20.1	19.7	19.2	18.3	17.9	17.1	16.3	15.8	15.1	14.4	13.6	12.3	10.6
E	70	23.1	23.0	22.1	22.2	21.6	20.9	20.3	19.8	19.4	19.0	18.1	17.7	17.0	16.3	15.7	14.9	14.2	13.4	11.9	10.4
P	80	22.7	22.6	21.7	21.9	21.2	20.6	20.0	19.5	19.1	18.7	18.0	17.7	16.9	16.2	15.5	14.7	14.0	12.9	11.5	10.1
T	90	22.4	22.2	21.4	21.7	20.9	20.3	19.7	19.3	18.9	18.5	17.8	17.6	16.9	16.0	15.3	14.5	13.7	12.5	11.1	9.9
H	100	22.1	21.9	21.1	21.4	20.6	20.0	19.5	19.0	18.6	18.3	17.6	17.5	16.7	15.9	15.2	14.2	13.4	11.9	10.7	9.7
	120	21.3	21.2	20.3	20.8	20.0	19.4	18.8	18.5	18.1	17.8	17.1	17.2	16.3	15.4	14.6	13.4	12.4	10.9	10.0	9.4
(M)	150	19.9	20.1	19.0	19.8	18.9	18.3	17.8	17.5	17.0	16.9	15.8	16.2	15.2	14.0	13.1	11.6	11.0	9.8	9.3	9.0
	200	17.4	17.6	16.6	17.5	16.6	15.8	15.5	15.1	14.5	14.3	12.8	13.1	12.2	11.2	10.6	9.8	9.5	8.8	8.5	8.3
	250	14.1	14.7	14.0	14.9	14.0	13.4	13.0	12.7	12.3	12.1	11.3	11.1	10.6	9.9	9.4	8.9	8.7	8.1	7.8	7.7
	300	11.5	12.1	11.8	12.4	12.0	11.6	11.5	11.2	10.9	10.7	10.2	10.0	9.5	9.0	8.4	8.0	7.8	7.4	7.1	7.1
	400	8.4	8.9	9.0	9.2	9.3	8.9	9.0	8.8	8.6	8.5	8.1	7.9	7.4	7.0	6.7	6.5	6.5	6.3	6.0	6.2
	500	6.8	6.7	6.9	6.9	6.9	6.8	6.8	6.7	6.7	6.5	6.1	6.1	5.9	5.7	5.5	5.5	5.7	5.5	5.3	5.6
N MI		50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM		93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614
D I S T A N C E																					

MEAN XBT TEMPERATURE, DEG-C

MID-JUNE

	0	25.0	25.0	24.5	24.1	23.9	23.4	23.0	22.4	21.9	21.2	20.5	20.0	19.5	18.8	18.2	17.5	16.7	15.8	14.5	13.2
	10	25.0	24.9	24.5	24.0	23.8	23.4	23.0	22.3	21.8	21.1	20.3	19.9	19.3	18.7	18.1	17.3	16.6	15.6	14.3	13.0
	20	24.9	24.8	24.3	23.9	23.7	23.3	22.8	22.2	21.8	21.1	20.2	19.7	19.0	18.4	17.8	17.0	16.3	15.3	14.1	12.8
	30	24.9	24.7	24.0	23.7	23.4	23.1	22.6	21.9	21.5	20.8	19.9	19.3	18.7	17.7	17.3	16.6	16.0	14.9	13.8	12.5
	40	24.6	24.5	23.6	23.4	23.1	22.6	22.1	21.3	21.0	20.4	19.4	18.7	18.2	17.1	16.6	16.0	15.4	14.5	13.3	11.9
	50	24.1	24.1	23.1	23.0	22.6	21.9	21.5	20.7	20.4	20.0	19.0	18.3	17.7	16.7	16.2	15.4	14.9	14.1	12.7	11.2
D	60	23.6	23.7	22.6	22.6	22.1	21.4	20.9	20.2	19.9	19.5	18.6	18.0	17.3	16.5	16.0	15.1	14.5	13.8	12.1	10.6
E	70	23.2	23.3	22.1	22.2	21.6	21.0	20.5	19.8	19.5	19.1	18.3	17.8	17.1	16.3	15.7	14.8	14.2	13.4	11.6	10.3
P	80	22.8	22.8	21.7	21.8	21.2	20.6	20.1	19.5	19.2	18.8	18.0	17.7	16.9	16.1	15.5	14.5	13.8	13.0	11.2	10.0
T	90	22.4	22.5	21.3	21.5	20.9	20.3	19.8	19.2	18.9	18.6	17.8	17.6	16.8	16.0	15.3	14.3	13.6	12.5	10.8	9.8
H	100	22.0	22.1	21.0	21.2	20.5	20.0	19.6	18.9	18.6	18.3	17.6	17.4	16.7	15.9	15.1	14.0	13.2	12.0	10.5	9.7
	120	21.2	21.3	20.3	20.6	19.9	19.4	19.0	18.4	18.1	17.9	17.0	17.2	16.3	15.4	14.5	13.2	12.3	11.0	9.9	9.3
(M)	150	19.9	20.2	19.0	19.6	18.8	18.4	17.9	17.5	17.1	17.0	15.8	16.2	15.2	14.1	13.0	11.5	10.9	10.0	9.3	8.9
	200	17.4	17.8	16.6	17.4	16.5	15.9	15.5	15.1	14.5	14.5	12.8	13.1	12.3	11.3	10.6	9.7	9.5	8.9	8.5	8.3
	250	14.2	14.8	14.0	14.8	13.9	13.5	13.0	12.7	12.4	12.2	11.2	11.2	10.7	10.0	9.4	8.8	8.6	8.2	7.8	7.6
	300	11.6	12.2	11.8	12.3	12.0	11.6	11.5	11.2	11.0	10.8	10.2	10.0	9.5	9.0	8.5	8.0	7.6	7.4	7.1	7.1
	400	8.4	9.0	9.0	9.1	9.3	8.9	9.0	8.8	8.7	8.6	8.1	7.9	7.5	7.0	6.8	6.4	6.4	6.3	6.1	6.1
	500	6.8	6.7	6.8	6.8	6.8	6.7	6.9	6.8	6.8	6.6	6.1	6.1	6.0	5.8	5.5	5.5	5.7	5.5	5.4	5.6
N MI		50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM		93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614
D I S T A N C E																					

MEAN XBT TEMPERATURE, DEG-C

01 JULY

0	25.4	25.3	24.9	24.5	24.3	23.9	23.6	22.9	22.6	22.0	21.4	21.0	20.6	19.9	19.2	18.6	17.7	16.8	15.4	14.0
10	25.4	25.2	24.8	24.5	24.3	23.9	23.5	22.8	22.5	21.9	21.3	20.9	20.4	19.7	19.1	18.4	17.6	16.6	15.2	13.9
20	25.3	25.2	24.7	24.4	24.2	23.8	23.4	22.7	22.4	21.8	21.2	20.7	20.1	19.4	18.8	18.0	17.3	16.2	14.9	13.6
30	25.3	25.1	24.5	24.1	24.0	23.6	23.2	22.4	22.2	21.6	20.9	20.1	19.7	18.5	18.1	17.5	17.0	15.7	14.6	13.0
40	25.0	24.8	24.1	23.8	23.5	23.1	22.6	21.8	21.6	21.1	20.2	19.2	18.8	17.6	17.1	16.4	16.0	15.1	13.7	12.2
50	24.4	24.4	23.5	23.2	22.9	22.3	21.9	21.1	20.8	20.3	19.5	18.6	18.0	17.0	16.5	15.7	15.2	14.5	12.9	11.3
D 60	23.8	24.0	22.8	22.6	22.2	21.6	21.2	20.4	20.2	19.7	19.0	18.2	17.6	16.7	16.2	15.2	14.7	13.9	12.2	10.7
E 70	23.4	23.5	22.3	22.1	21.6	21.1	20.7	19.9	19.7	19.3	18.5	17.9	17.2	16.4	15.8	14.8	14.2	13.4	11.5	10.3
P 80	22.9	23.1	21.8	21.7	21.1	20.7	20.3	19.5	19.3	18.9	18.2	17.7	16.9	16.1	15.5	14.5	13.8	12.9	11.0	10.0
T 90	22.4	22.7	21.4	21.3	20.7	20.4	19.9	19.1	19.0	18.6	17.9	17.5	16.7	16.0	15.3	14.2	13.5	12.4	10.7	9.8
H 100	22.0	22.2	21.1	21.0	20.4	20.1	19.6	18.8	18.7	18.3	17.7	17.3	16.6	15.8	15.1	13.9	13.2	12.0	10.4	9.6
120	21.2	21.4	20.4	20.4	19.8	19.5	19.1	18.4	18.2	18.0	17.1	17.0	16.3	15.4	14.4	13.1	12.3	11.1	9.9	9.3
(M) 150	20.0	20.3	19.2	19.4	18.8	18.6	18.0	17.4	17.2	17.1	15.9	16.0	15.1	14.2	12.9	11.6	10.9	10.1	9.2	8.9
200	17.5	17.9	16.8	17.1	16.5	16.1	15.5	15.1	14.6	14.6	12.9	13.1	12.3	11.5	10.5	9.8	9.5	9.0	8.5	8.2
250	14.3	14.8	14.1	14.4	13.7	13.7	13.0	12.7	12.4	12.3	11.3	11.2	10.7	10.2	9.4	8.8	8.7	8.3	7.8	7.6
300	11.6	12.2	11.9	12.1	11.9	11.7	11.5	11.1	11.0	10.9	10.2	10.0	9.6	9.0	8.4	8.0	7.8	7.5	7.2	7.0
400	8.5	8.9	8.9	9.0	9.2	9.0	9.0	8.8	8.7	8.7	8.2	8.0	7.6	7.1	6.8	6.5	6.4	6.3	6.2	6.0
500	6.7	6.6	6.7	6.7	6.6	7.0	6.9	6.8	6.9	6.6	6.2	6.2	6.0	5.8	5.7	5.5	5.5	5.5	5.5	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KH	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

MID-JULY

0	25.7	25.4	25.1	24.8	24.6	24.3	24.0	23.4	23.0	22.6	22.1	21.7	21.3	20.6	20.0	19.4	18.5	17.5	16.2	14.7
10	25.7	25.4	25.1	24.8	24.6	24.2	23.9	23.3	23.0	22.5	22.0	21.6	21.1	20.5	19.8	19.2	18.4	17.3	15.9	14.5
20	25.6	25.3	25.0	24.7	24.5	24.1	23.8	23.1	22.9	22.4	21.9	21.3	20.8	20.2	19.6	18.8	18.1	17.0	15.6	14.1
30	25.6	25.3	24.8	24.5	24.3	24.0	23.6	22.8	22.7	22.2	21.6	20.7	20.4	19.2	18.8	18.1	17.7	16.5	15.3	13.4
40	25.4	25.1	24.5	24.2	23.8	23.5	23.0	22.2	22.0	21.6	20.8	19.7	19.2	18.1	17.5	16.8	16.5	15.6	14.3	12.4
50	24.8	24.7	23.9	23.5	23.1	22.6	22.2	21.5	21.1	20.5	19.8	18.8	18.3	17.3	16.7	15.9	15.5	14.8	13.4	11.4
D 60	24.1	24.2	23.1	22.7	22.2	21.8	21.5	20.7	20.4	19.8	19.3	18.4	17.7	16.9	16.3	15.4	14.9	14.0	12.6	10.8
E 70	23.5	23.6	22.5	22.2	21.6	21.3	20.9	20.0	19.9	19.3	18.8	18.0	17.3	16.5	15.9	14.9	14.4	13.4	11.8	10.3
P 80	23.0	23.1	22.0	21.7	21.1	20.9	20.4	19.5	19.5	18.9	18.4	17.7	16.9	16.2	15.6	14.5	13.8	12.8	11.2	10.0
T 90	22.5	22.7	21.6	21.3	20.7	20.5	20.0	19.1	19.1	18.5	18.1	17.5	16.7	16.0	15.3	14.3	13.5	12.3	10.8	9.8
H 100	22.1	22.2	21.2	20.9	20.3	20.2	19.6	18.8	18.8	18.2	17.8	17.3	16.6	15.9	15.1	13.9	13.2	11.9	10.5	9.6
120	21.2	21.4	20.5	20.2	19.7	19.6	19.1	18.3	18.3	17.9	17.2	17.0	16.3	15.5	14.5	13.2	12.4	11.2	10.0	9.3
(M) 150	20.0	20.2	19.4	19.2	18.7	18.7	18.1	17.4	17.3	17.0	16.1	15.9	15.1	14.2	12.8	11.8	11.0	10.1	9.3	8.8
200	17.4	17.8	16.9	16.8	16.4	16.3	15.6	15.0	14.6	14.6	13.1	13.1	12.3	11.7	10.5	9.9	9.5	9.1	8.6	8.2
250	14.3	14.7	14.1	14.0	13.6	13.8	13.1	12.6	12.4	12.3	11.4	11.2	10.7	10.3	9.4	8.9	8.7	8.3	7.9	7.5
300	11.7	12.0	11.9	11.8	11.8	11.8	11.4	11.1	11.0	10.9	10.3	10.0	9.6	9.1	8.4	8.1	7.8	7.5	7.3	6.9
400	8.6	8.9	8.8	8.9	9.0	9.1	9.0	8.8	8.7	8.7	8.2	8.0	7.6	7.2	6.8	6.5	6.4	6.4	6.3	6.0
500	6.7	6.6	6.6	6.6	6.6	7.1	6.9	6.8	6.8	6.6	6.3	6.2	6.1	5.8	5.8	5.5	5.5	5.5	5.6	5.6
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KH	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

01 AUGUST

	0	25.9	25.6	25.2	25.1	24.9	24.5	24.2	23.8	23.5	23.1	22.7	22.2	22.0	21.3	20.6	20.2	19.3	18.1	16.9	15.3
	10	25.9	25.6	25.3	25.1	24.9	24.5	24.2	23.8	23.4	23.0	22.6	22.1	21.8	21.2	20.5	20.0	19.1	17.9	16.7	15.1
	20	25.9	25.5	25.2	25.0	24.8	24.4	24.1	23.6	23.3	22.9	22.5	21.9	21.5	20.9	20.3	19.6	18.9	17.7	16.4	14.6
	30	25.9	25.5	25.1	24.9	24.7	24.3	23.9	23.3	23.1	22.7	22.2	21.4	20.9	20.0	19.4	18.8	18.3	17.2	16.1	13.7
	40	25.7	25.3	24.9	24.6	24.2	23.9	23.3	22.7	22.5	22.0	21.4	20.2	19.6	18.7	18.1	17.2	17.0	16.2	15.1	12.5
	50	25.2	24.9	24.3	23.8	23.3	22.9	22.5	21.9	21.5	20.7	20.2	19.2	18.5	17.6	17.0	16.1	15.8	15.0	14.0	11.5
D	60	24.5	24.3	23.5	23.0	22.3	22.1	21.6	20.9	20.6	19.8	19.5	18.7	17.8	17.0	16.5	15.6	15.1	14.1	13.2	11.0
E	70	23.7	23.6	22.8	22.3	21.6	21.5	21.0	20.2	20.1	19.3	18.9	18.2	17.4	16.7	16.1	15.1	14.5	13.4	12.3	10.4
P	80	23.1	23.1	22.3	21.8	21.1	21.0	20.5	19.7	19.7	18.8	18.6	17.9	17.0	16.3	15.8	14.7	13.9	12.8	11.6	10.1
T	90	22.7	22.6	21.8	21.3	20.7	20.6	20.0	19.3	19.3	18.5	18.3	17.6	16.7	16.1	15.5	14.4	13.6	12.3	11.2	9.9
H	100	22.2	22.2	21.4	20.9	20.3	20.2	19.6	18.9	19.0	18.2	18.0	17.4	16.6	15.9	15.3	14.1	13.3	11.9	10.8	9.6
	120	21.4	21.2	20.6	20.1	19.7	19.6	19.0	18.3	18.3	17.8	17.4	17.0	16.3	15.6	14.6	13.4	12.5	11.2	10.3	9.2
(M)	150	20.1	20.0	19.5	19.0	18.6	18.7	18.1	17.4	17.4	16.9	16.3	16.0	15.1	14.3	12.8	12.0	11.0	10.1	9.5	8.8
	200	17.5	17.6	17.1	16.5	16.3	16.4	15.6	14.9	14.7	14.4	13.4	13.1	12.2	11.8	10.5	10.1	9.5	9.1	8.8	8.2
	250	14.4	14.5	14.2	13.7	13.6	13.8	13.1	12.5	12.4	12.2	11.5	11.2	10.7	10.3	9.4	9.1	8.7	8.4	8.0	7.5
	300	11.8	11.8	11.8	11.6	11.7	11.8	11.3	11.0	10.9	10.8	10.3	10.0	9.6	9.2	8.5	8.2	7.8	7.6	7.4	6.9
	400	8.7	8.7	8.7	8.9	8.9	9.1	8.9	8.7	8.6	8.6	8.2	8.0	7.6	7.3	6.8	6.6	6.4	6.4	6.4	6.1
	500	6.6	6.6	6.6	6.6	6.6	7.2	6.9	6.7	6.8	6.6	6.3	6.2	6.0	5.8	5.8	5.6	5.4	5.5	5.7	5.6
N MI		50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM		93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

MID-AUGUST

	0	26.2	25.8	25.5	25.4	25.2	24.8	24.5	24.3	23.8	23.5	23.1	22.6	22.4	21.9	21.1	20.7	19.8	18.6	17.5	15.8
	10	26.2	25.7	25.5	25.4	25.1	24.8	24.5	24.2	23.7	23.5	23.1	22.5	22.2	21.8	21.0	20.5	19.7	18.4	17.3	15.6
	20	26.2	25.7	25.5	25.3	25.1	24.7	24.4	24.1	23.6	23.4	23.0	22.4	21.9	21.5	20.8	20.1	19.4	18.2	17.1	14.9
	30	26.1	25.7	25.4	25.3	25.0	24.6	24.2	23.9	23.5	23.2	22.7	21.9	21.4	20.7	20.0	19.4	18.8	17.9	16.7	13.8
	40	26.0	25.6	25.3	25.1	24.5	24.2	23.7	23.3	23.0	22.5	21.9	20.9	19.9	19.4	18.7	17.8	17.4	16.6	15.8	12.5
	50	25.5	25.1	24.7	24.3	23.5	23.3	22.8	22.4	21.9	20.9	20.5	19.8	18.7	17.9	17.3	16.5	16.0	15.3	14.7	11.5
D	60	24.8	24.4	23.8	23.3	22.5	22.3	21.8	21.3	20.9	19.8	19.6	19.0	17.9	17.2	16.6	15.8	15.2	14.2	13.8	11.1
E	70	23.9	23.6	23.0	22.6	21.7	21.6	21.0	20.5	20.3	19.2	19.0	18.5	17.4	16.8	16.2	15.3	14.6	13.5	12.9	10.4
P	80	23.3	22.9	22.4	22.0	21.2	21.1	20.5	19.9	19.8	18.8	18.7	18.1	17.1	16.5	15.9	14.9	14.0	12.9	12.1	10.1
T	90	22.9	22.4	21.9	21.5	20.8	20.6	20.0	19.5	19.4	18.5	18.4	17.8	16.8	16.3	15.6	14.6	13.6	12.4	11.6	9.9
H	100	22.4	22.0	21.5	21.0	20.3	20.3	19.6	19.1	19.1	18.2	18.1	17.5	16.6	16.1	15.4	14.3	13.3	12.0	11.2	9.6
	120	21.5	21.0	20.6	20.1	19.6	19.6	19.0	18.4	18.4	17.6	17.5	17.1	16.3	15.6	14.8	13.6	12.6	11.2	10.5	9.2
(M)	150	20.2	19.8	19.5	18.9	18.6	18.6	18.0	17.4	17.4	16.7	16.5	16.1	15.0	14.3	13.0	12.2	11.0	10.1	9.7	8.8
	200	17.5	17.3	17.1	16.4	16.3	16.3	15.7	14.9	14.7	14.1	13.7	13.2	12.2	11.8	10.6	10.2	9.4	9.1	9.0	8.2
	250	14.5	14.3	14.2	13.5	13.7	13.6	13.1	12.5	12.3	12.0	11.6	11.2	10.7	10.3	9.4	9.2	8.7	8.4	8.2	7.5
	300	11.9	11.6	11.7	11.5	11.8	11.7	11.3	11.0	10.9	10.7	10.4	10.1	9.6	9.2	8.5	8.2	7.8	7.6	7.5	6.9
	400	8.8	8.6	8.7	8.9	8.9	9.1	8.9	8.7	8.6	8.5	8.2	8.0	7.6	7.3	6.8	6.7	6.4	6.5	6.4	6.2
	500	6.7	6.7	6.6	6.6	6.6	7.2	6.9	6.7	6.7	6.5	6.4	6.1	6.0	5.7	5.8	5.6	5.4	5.6	5.7	5.7
N MI		50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM		93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

01 SEPTEMBER

0	26.3	26.0	25.7	25.7	25.4	25.1	24.8	24.6	24.1	23.8	23.4	22.9	22.6	22.2	21.4	20.9	20.1	18.8	17.8	16.1
10	26.4	26.0	25.7	25.6	25.4	25.1	24.7	24.5	24.0	23.8	23.3	22.8	22.5	22.1	21.3	20.7	20.0	18.7	17.7	15.8
20	26.3	25.9	25.7	25.6	25.3	25.0	24.6	24.4	23.9	23.7	23.3	22.7	22.3	21.9	21.1	20.4	19.7	18.6	17.5	15.0
30	26.3	25.9	25.7	25.6	25.2	24.9	24.5	24.3	23.8	23.5	22.9	22.4	21.7	21.3	20.5	19.8	19.1	18.3	17.2	13.9
40	26.2	25.8	25.5	25.4	24.8	24.6	24.0	23.8	23.4	22.9	22.2	21.5	20.4	20.0	19.3	18.4	17.7	17.1	16.4	12.5
50	25.8	25.3	25.1	24.7	23.9	23.7	23.1	22.4	22.3	21.3	20.8	20.4	19.0	18.3	17.7	16.9	16.2	15.6	15.2	11.5
60	25.1	24.5	24.2	23.8	22.8	22.6	21.1	21.6	21.1	20.1	19.7	19.4	18.0	17.3	16.7	15.9	15.2	14.4	14.2	11.0
70	24.1	23.6	23.3	22.9	21.9	21.7	21.0	20.7	20.3	19.2	19.0	18.7	17.5	16.8	16.3	15.4	14.6	13.6	13.3	10.5
80	23.4	22.9	22.5	22.2	21.4	21.1	20.4	20.1	19.8	18.8	18.7	18.3	17.1	16.6	16.0	15.1	14.0	13.0	12.4	10.1
90	23.1	22.3	22.0	21.6	20.9	20.6	20.0	19.7	19.4	18.5	18.4	18.0	16.9	16.4	15.7	14.7	13.6	12.5	11.9	9.9
100	22.5	21.9	21.5	21.2	20.4	20.2	19.6	19.3	19.0	18.2	18.1	17.8	16.7	16.2	15.5	14.4	13.2	12.0	11.4	9.6
120	21.6	20.9	20.6	20.2	19.7	19.5	18.9	18.5	18.3	17.5	17.6	17.2	16.2	15.6	14.9	13.7	12.5	11.3	10.7	9.2
150	20.2	19.6	19.3	19.0	18.6	18.4	18.0	17.5	17.3	16.6	16.5	16.1	15.0	14.2	13.2	12.1	10.9	10.1	9.8	8.8
200	17.7	17.2	17.0	16.5	16.4	16.1	15.8	15.0	14.7	13.9	13.9	13.3	12.1	11.6	10.7	10.2	9.4	9.1	9.0	8.2
250	14.7	14.2	14.1	13.6	13.9	13.5	13.2	12.6	12.3	11.8	11.7	11.2	10.6	10.2	9.5	9.2	8.6	8.4	8.3	7.5
300	12.0	11.6	11.6	11.6	11.9	11.6	11.4	11.1	10.9	10.6	10.4	10.1	9.5	9.2	8.5	8.2	7.7	7.7	7.5	7.0
400	8.9	8.6	8.6	8.9	9.0	9.1	8.9	8.7	8.6	8.3	8.2	8.0	7.5	7.2	6.8	6.6	6.4	6.5	6.4	6.3
500	6.7	6.7	6.6	6.7	6.7	7.1	6.8	6.7	6.6	6.5	6.4	6.1	5.9	5.6	5.7	5.6	5.5	5.6	5.7	5.7
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

MID-SEPTEMBER

0	26.4	26.2	25.9	25.9	25.6	25.3	25.0	24.7	24.2	23.9	23.4	23.0	22.5	22.2	21.5	20.7	20.1	18.9	17.8	16.2
10	26.5	26.2	25.9	25.8	25.6	25.3	24.9	24.7	24.2	23.9	23.4	23.0	22.5	22.1	21.4	20.6	20.0	18.8	17.8	15.9
20	26.4	26.1	25.9	25.8	25.6	25.3	24.8	24.6	24.1	23.8	23.3	22.9	22.4	22.0	21.3	20.4	19.8	18.7	17.6	15.2
30	26.4	26.1	25.9	25.7	25.5	25.2	24.7	24.5	24.0	23.7	23.0	22.7	21.9	21.6	20.8	19.9	19.2	18.5	17.4	14.0
40	26.3	26.0	25.7	25.6	25.1	24.9	24.4	24.1	23.7	23.2	22.4	22.0	20.8	20.5	19.8	19.0	18.0	17.4	16.6	12.6
50	26.0	25.5	25.3	25.1	24.2	24.2	23.6	23.2	22.7	21.8	21.1	21.0	19.4	18.7	18.1	17.3	16.5	15.9	15.3	11.5
60	25.4	24.8	24.5	24.3	23.2	23.0	22.2	22.0	21.4	20.5	19.9	19.8	18.2	17.5	16.9	16.1	15.2	14.7	14.2	11.0
70	24.4	23.8	23.5	23.2	22.3	21.9	21.1	21.1	20.4	19.4	19.0	19.0	17.5	16.9	16.3	15.4	14.5	13.8	13.3	10.4
80	23.6	23.0	22.6	22.4	21.6	21.1	20.4	20.4	19.7	18.8	18.6	18.4	17.2	16.6	16.0	15.1	13.9	13.1	12.5	10.1
90	23.2	22.4	21.9	21.8	21.0	20.6	20.1	19.9	19.3	18.5	18.3	18.1	16.9	16.4	15.7	14.7	13.5	12.6	12.0	9.9
100	22.6	21.9	21.4	21.3	20.5	20.2	19.7	19.5	18.9	18.2	18.0	17.9	16.7	16.2	15.5	14.4	13.1	12.1	11.5	9.6
120	21.6	20.9	20.5	20.4	19.7	19.4	18.9	18.7	18.2	17.5	17.5	17.3	16.2	15.5	14.9	13.5	12.3	11.3	10.7	9.2
150	20.1	19.6	19.2	19.1	18.6	18.3	17.9	17.6	17.2	16.4	16.4	16.1	14.9	14.0	13.4	11.9	10.7	10.1	9.8	8.7
200	17.6	17.1	16.9	16.8	16.4	15.9	15.8	15.1	14.7	13.7	13.8	13.3	12.1	11.4	10.8	10.1	9.3	9.1	9.0	8.1
250	14.9	14.1	14.0	13.9	14.0	13.4	13.3	12.7	12.3	11.7	11.6	11.2	10.6	10.0	9.5	9.2	8.5	8.3	8.3	7.5
300	12.1	11.7	11.6	11.8	11.9	11.5	11.5	11.2	10.9	10.4	10.4	10.1	9.5	9.1	8.6	8.1	7.6	7.6	7.5	7.0
400	9.0	8.6	8.7	9.0	9.1	9.0	8.9	8.8	8.6	8.2	8.2	7.9	7.5	7.1	6.8	6.5	6.3	6.5	6.3	6.3
500	6.8	6.7	6.7	6.9	6.8	7.0	6.8	6.7	6.5	6.4	6.3	6.1	5.9	5.6	5.6	5.6	5.5	5.5	5.6	5.7
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

01 OCTOBER

0	26.4	26.2	26.1	25.9	25.7	25.4	25.0	24.6	24.2	23.8	23.2	22.9	22.3	21.9	21.3	20.3	19.9	18.7	17.6	16.0
10	26.4	26.2	26.0	25.8	25.7	25.4	25.0	24.6	24.1	23.8	23.2	22.9	22.3	21.9	21.2	20.2	19.7	18.6	17.5	15.8
20	26.4	26.2	26.0	25.8	25.6	25.4	24.9	24.5	24.1	23.8	23.1	22.8	22.3	21.8	21.1	20.1	19.6	18.6	17.4	15.2
30	26.4	26.2	25.9	25.7	25.6	25.3	24.8	24.5	24.1	23.7	22.9	22.7	21.9	21.5	20.9	19.9	19.1	18.4	17.2	14.1
40	26.3	26.1	25.8	25.6	25.3	25.1	24.6	24.2	23.8	23.3	22.4	22.3	21.2	20.7	20.1	19.3	18.2	17.6	16.4	12.8
50	26.1	25.7	25.5	25.3	24.6	24.5	23.9	23.4	23.0	22.3	21.3	21.4	19.9	19.1	18.6	17.6	16.8	16.3	15.1	11.5
D 60	25.6	25.1	24.7	24.6	23.7	23.4	22.5	22.4	21.7	21.0	20.0	20.2	18.5	17.7	17.1	16.2	15.3	15.0	14.0	10.8
E 70	24.6	24.2	23.6	23.5	22.6	22.0	21.4	21.4	20.4	19.7	19.0	19.2	17.6	16.9	16.3	15.4	14.4	13.9	13.0	10.4
F 80	23.7	23.3	22.7	22.6	21.7	21.2	20.6	20.6	19.6	18.9	18.5	18.5	17.1	16.6	15.9	14.9	13.8	13.2	12.2	10.0
T 90	23.2	22.6	22.0	21.9	21.1	20.6	20.1	20.0	19.1	18.5	18.1	18.1	16.9	16.3	15.6	14.5	13.4	12.7	11.7	9.8
H 100	22.6	22.1	21.4	21.4	20.6	20.1	19.7	19.6	18.7	18.1	17.8	17.9	16.7	16.1	15.4	14.1	13.0	12.1	11.2	9.6
120	21.6	21.1	20.5	20.5	19.8	19.3	19.0	18.8	18.1	17.5	17.3	17.2	16.1	15.4	14.7	13.2	12.0	11.3	10.6	9.2
(M) 150	20.3	19.8	19.2	19.3	18.6	18.2	17.9	17.7	17.1	16.4	16.2	16.0	14.8	13.8	13.4	11.5	10.6	10.1	9.7	8.7
200	17.9	17.2	16.8	17.0	16.4	15.8	15.8	15.3	14.5	13.7	13.6	13.1	12.1	11.2	10.8	9.9	9.3	9.0	8.8	8.1
250	14.9	14.2	14.0	14.2	14.1	13.4	13.3	12.9	12.3	11.6	11.5	11.2	10.5	9.9	9.5	9.0	8.5	8.3	8.1	7.4
300	12.2	11.8	11.7	11.9	11.9	11.5	11.5	11.2	10.9	10.4	10.3	10.0	9.5	8.9	8.6	7.9	7.6	7.6	7.4	7.0
400	8.9	8.6	8.7	9.1	9.2	9.0	8.9	8.8	8.7	8.2	8.1	7.8	7.5	7.0	6.8	6.4	6.3	6.4	6.3	6.2
500	6.9	6.7	6.8	6.9	6.8	6.9	6.8	6.8	6.5	6.4	6.2	6.1	6.0	5.6	5.6	5.5	5.5	5.5	5.5	5.7
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

MID-OCTOBER

0	26.3	26.1	26.0	25.7	25.5	25.3	24.8	24.3	23.9	23.5	22.8	22.5	21.9	21.4	20.8	19.7	19.3	18.3	17.0	15.6
10	26.3	26.1	25.9	25.7	25.5	25.3	24.8	24.2	23.9	23.4	22.8	22.5	21.9	21.3	20.7	19.6	19.2	18.3	17.0	15.5
20	26.3	26.1	25.9	25.6	25.5	25.3	24.7	24.2	23.9	23.4	22.7	22.5	21.9	21.3	20.7	19.6	19.1	18.2	16.9	15.1
30	26.2	26.1	25.8	25.5	25.5	25.2	24.7	24.2	23.9	23.4	22.6	22.5	21.7	21.2	20.6	19.5	18.9	18.1	16.7	14.2
40	26.2	26.0	25.7	25.4	25.3	25.1	24.6	24.0	23.7	23.2	22.3	22.2	21.3	20.7	20.1	19.3	18.3	17.6	16.0	13.0
50	26.0	25.8	25.5	25.2	24.8	24.7	24.1	23.4	23.1	22.6	21.4	21.5	20.3	19.4	18.8	17.8	17.0	16.5	14.8	11.6
D 60	25.6	25.3	24.8	24.7	24.0	23.7	22.9	22.7	21.9	21.4	20.3	20.4	18.9	17.9	17.3	16.3	15.6	15.2	13.5	10.7
E 70	24.9	24.6	23.8	23.7	22.9	22.3	21.8	21.7	20.6	20.0	19.2	19.3	17.8	17.1	16.3	15.2	14.4	13.9	12.6	10.3
F 80	24.0	23.8	22.8	22.8	21.9	21.3	20.9	20.7	19.7	19.1	18.5	18.5	17.2	16.6	15.8	14.6	13.8	13.1	11.8	10.0
T 90	23.3	23.0	22.1	22.0	21.2	20.7	20.3	20.1	19.1	18.5	18.1	18.1	16.8	16.3	15.5	14.3	13.4	12.6	11.3	9.7
H 100	22.5	22.3	21.5	21.4	20.6	20.1	19.8	19.7	18.7	18.1	17.7	17.8	16.6	16.0	15.2	13.8	12.9	12.0	10.9	9.5
120	21.6	21.3	20.7	20.6	19.8	19.3	19.0	18.9	18.0	17.5	17.1	17.1	16.1	15.3	14.5	12.9	11.9	11.2	10.3	9.2
(M) 150	20.3	19.9	19.4	19.4	18.7	18.2	17.9	17.8	17.0	16.4	16.0	15.8	14.8	13.7	13.3	11.2	10.5	10.1	9.5	8.6
200	17.9	17.3	17.0	17.2	16.4	15.8	15.8	15.5	14.4	13.7	13.3	12.9	12.1	11.1	10.8	9.7	9.3	9.0	8.6	8.0
250	14.8	14.3	14.2	14.4	14.0	13.4	13.3	13.0	12.3	11.7	11.4	11.1	10.6	9.8	9.5	8.9	8.4	8.2	7.9	7.4
300	12.1	11.9	11.8	12.1	11.8	11.5	11.5	11.3	10.9	10.4	10.2	9.9	9.5	8.9	8.6	7.8	7.6	7.5	7.3	6.9
400	8.8	8.7	8.7	9.1	9.2	8.9	8.9	8.8	8.7	8.2	8.1	7.7	7.5	7.0	6.8	6.3	6.3	6.3	6.3	6.1
500	6.8	6.7	6.8	6.9	6.8	6.8	6.8	6.8	6.6	6.3	6.2	6.0	6.0	5.6	5.6	5.5	5.5	5.5	5.4	5.6
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

01 NOVEMBER

0	26.0	25.8	25.6	25.3	25.2	24.9	24.4	23.8	23.5	22.9	22.2	21.9	21.3	20.6	20.1	19.0	18.6	17.7	16.3	15.1
10	26.0	25.8	25.6	25.3	25.1	24.9	24.4	23.8	23.5	22.8	22.2	21.9	21.3	20.6	20.0	19.0	18.6	17.7	16.3	15.0
20	26.0	25.8	25.6	25.3	25.1	24.9	24.4	23.7	23.5	22.8	22.2	21.9	21.3	20.6	20.0	19.0	18.6	17.7	16.2	14.8
30	25.9	25.8	25.6	25.2	25.1	24.9	24.4	23.7	23.4	22.8	22.1	21.9	21.3	20.6	20.0	19.0	18.5	17.6	16.1	14.1
40	25.9	25.7	25.5	25.1	25.0	24.8	24.4	23.7	23.4	22.8	22.0	21.8	21.1	20.4	19.7	19.0	18.2	17.4	15.4	13.1
50	25.8	25.6	25.3	25.0	24.8	24.6	24.0	23.3	23.0	22.5	21.4	21.4	20.4	19.5	18.9	17.9	17.2	16.6	14.5	11.7
D 60	25.5	25.4	24.7	24.6	24.2	23.8	23.1	22.8	22.1	21.6	20.4	20.4	19.3	18.2	17.6	16.3	15.8	15.4	13.2	10.7
E 70	25.1	24.9	23.9	23.8	23.1	22.5	22.3	21.9	20.9	20.3	19.4	19.3	18.1	17.4	16.4	15.1	14.7	13.9	12.2	10.2
P 80	24.2	24.2	23.1	22.9	22.0	21.6	21.3	20.9	20.0	19.3	18.7	18.5	17.3	16.7	15.7	14.5	13.9	13.1	11.4	9.9
T 90	23.4	23.4	22.4	22.1	21.2	20.8	20.4	20.3	19.3	18.6	18.2	18.0	16.8	16.3	15.4	14.0	13.3	12.4	10.9	9.7
H 100	22.6	22.6	21.8	21.5	20.7	20.3	19.9	19.7	18.7	18.1	17.7	17.6	16.5	15.9	15.1	13.5	12.8	11.9	10.5	9.4
120	21.6	21.4	20.9	20.6	19.8	19.4	19.1	18.9	18.0	17.5	17.0	16.9	16.0	15.3	14.4	12.6	11.9	11.1	10.0	9.1
(M) 150	20.2	20.1	19.7	19.4	18.6	18.2	18.0	17.8	16.9	16.3	15.9	15.6	14.7	13.7	13.1	11.1	10.6	10.0	9.3	8.6
200	17.7	17.4	17.3	17.1	16.3	15.8	15.7	15.6	14.2	13.8	13.0	12.7	12.1	11.1	10.7	9.6	9.3	9.0	8.5	7.9
250	14.6	14.3	14.4	14.3	13.8	13.4	13.2	13.0	12.2	11.7	11.3	11.0	10.6	9.8	9.5	8.8	8.5	8.2	7.8	7.3
300	11.9	11.9	11.9	12.0	11.7	11.5	11.4	11.3	10.9	10.5	10.1	9.8	9.5	8.8	8.5	7.8	7.6	7.4	7.2	6.8
400	8.7	8.7	8.8	9.1	9.1	9.0	8.9	8.8	8.7	8.3	7.9	7.7	7.6	7.0	6.8	6.3	6.3	6.2	6.3	6.0
500	6.7	6.6	6.8	6.9	6.8	6.7	6.8	6.8	6.6	6.3	6.1	6.0	6.1	5.7	5.6	5.6	5.5	5.5	5.5	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

MID-NOVEMBER

0	25.6	25.3	25.1	24.8	24.6	24.3	23.8	23.2	22.9	22.1	21.5	21.1	20.5	19.8	19.2	18.3	17.8	17.0	15.6	14.3
10	25.5	25.3	25.1	24.8	24.6	24.3	23.8	23.2	22.9	22.1	21.4	21.1	20.5	19.8	19.1	18.3	17.8	17.0	15.6	14.3
20	25.5	25.3	25.1	24.8	24.6	24.3	23.8	23.2	22.9	22.1	21.5	21.2	20.6	19.8	19.1	18.3	17.9	17.0	15.5	14.3
30	25.5	25.3	25.1	24.7	24.6	24.3	23.8	23.2	22.8	22.1	21.5	21.1	20.6	19.9	19.2	18.3	17.9	17.0	15.4	13.8
40	25.5	25.3	25.0	24.7	24.5	24.4	23.8	23.1	22.8	22.1	21.5	21.1	20.6	19.9	19.1	18.4	17.8	17.0	14.9	13.1
50	25.4	25.3	24.9	24.6	24.5	24.2	23.7	23.1	22.6	22.0	21.1	20.9	20.3	19.4	18.7	17.7	17.2	16.5	14.3	11.8
D 60	25.3	25.2	24.6	24.3	24.0	23.7	23.2	22.8	22.1	21.5	20.5	20.2	19.5	18.5	17.7	16.4	16.1	15.3	13.1	10.8
E 70	25.1	25.0	24.0	23.8	23.1	22.7	22.6	22.1	21.2	20.5	19.7	19.3	18.4	17.7	16.6	15.2	15.0	14.0	12.1	10.2
P 80	24.4	24.4	23.3	23.1	22.1	21.8	21.7	21.1	20.3	19.5	19.0	18.6	17.5	17.0	15.8	14.5	14.1	13.0	11.3	9.9
T 90	23.5	23.6	22.7	22.2	21.3	21.1	20.7	20.4	19.6	18.7	18.5	18.0	16.9	16.4	15.4	13.9	13.3	12.3	10.7	9.7
H 100	22.7	22.8	22.1	21.6	20.7	20.4	20.0	19.8	19.0	18.1	17.9	17.5	16.5	15.9	15.0	13.4	12.8	11.8	10.3	9.4
120	21.5	21.5	21.1	20.6	19.8	19.4	19.0	18.9	18.1	17.5	17.1	16.8	16.0	15.3	14.3	12.6	11.9	10.9	9.8	9.1
(M) 150	20.2	20.1	19.9	19.3	18.6	18.2	17.9	17.8	16.9	16.3	15.9	15.4	14.7	13.7	12.9	11.2	10.7	10.0	9.2	8.6
200	17.5	17.3	17.5	17.0	16.2	15.9	15.5	15.5	14.2	13.8	12.9	12.6	12.1	11.2	10.7	9.7	9.3	8.9	8.4	7.9
250	14.3	14.2	14.6	14.1	13.7	13.5	13.0	12.9	12.2	11.7	11.2	10.9	10.6	9.9	9.5	8.8	8.5	8.1	7.7	7.3
300	11.7	11.7	12.0	11.9	11.6	11.6	11.3	11.3	10.9	10.5	10.0	9.8	9.6	8.9	8.5	7.9	7.7	7.4	7.2	6.8
400	8.5	8.7	8.8	9.1	9.0	9.0	8.9	8.8	8.6	8.3	7.9	7.6	7.6	7.1	6.8	6.4	6.3	6.2	6.3	6.0
500	6.6	6.6	6.7	6.8	6.8	6.8	6.7	6.7	6.6	6.3	6.1	6.1	6.1	5.8	5.7	5.6	5.5	5.5	5.5	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614

D I S T A N C E

MEAN XBT TEMPERATURE, DEG-C

01 DECEMBER

0	25.1	24.8	24.5	24.2	23.9	23.7	23.2	22.6	22.2	21.3	20.7	20.4	19.8	19.1	18.3	17.7	17.1	16.3	14.9	13.6
10	25.1	24.8	24.5	24.2	23.9	23.7	23.1	22.6	22.2	21.3	20.7	20.4	19.8	19.1	18.3	17.7	17.1	16.3	14.9	13.6
20	25.1	24.8	24.5	24.2	23.9	23.7	23.2	22.6	22.2	21.3	20.8	20.4	19.8	19.1	18.3	17.6	17.1	16.3	14.9	13.6
30	25.1	24.8	24.5	24.2	23.9	23.7	23.2	22.6	22.2	21.3	20.8	20.4	19.8	19.1	18.3	17.6	17.3	16.4	14.8	13.4
40	25.0	24.8	24.5	24.2	23.9	23.7	23.2	22.6	22.2	21.3	20.9	20.4	19.9	19.2	18.4	17.7	17.3	16.4	14.6	12.9
50	25.0	24.8	24.5	24.2	24.0	23.7	23.2	22.7	22.2	21.3	20.6	20.3	19.8	19.1	18.3	17.4	17.0	16.2	14.2	11.9
D 60	25.0	24.9	24.3	24.0	23.7	23.4	23.0	22.5	22.0	21.1	20.4	20.0	19.4	18.6	17.7	16.4	16.2	15.2	13.2	10.9
E 70	25.0	24.8	23.9	23.7	23.0	22.7	22.7	22.0	21.4	20.4	19.8	19.3	18.6	18.0	16.8	15.3	15.3	14.1	12.2	10.3
F 80	24.4	24.3	23.5	23.1	22.2	22.0	21.9	21.3	20.7	19.6	19.4	18.7	17.7	17.1	16.0	14.7	14.3	13.1	11.3	9.9
T 90	23.5	23.6	22.9	22.4	21.4	21.3	20.9	20.6	19.9	18.8	18.9	18.1	17.1	16.6	15.5	14.0	13.3	12.3	10.8	9.7
H 100	22.8	22.8	22.4	21.7	20.8	20.6	20.1	19.9	19.3	18.3	18.2	17.5	16.7	16.0	15.0	13.5	12.8	11.7	10.4	9.4
120	21.5	21.4	21.3	20.6	19.9	19.5	19.0	18.9	18.2	17.4	17.3	16.8	16.1	15.3	14.3	12.7	12.0	10.8	9.7	9.0
(M) 150	20.1	19.9	20.0	19.3	18.6	18.2	17.9	17.7	16.9	16.2	16.0	15.4	14.7	13.8	12.8	11.3	10.7	9.9	9.1	8.6
200	17.3	17.3	17.7	16.7	16.1	15.9	15.4	15.4	14.2	13.7	12.9	12.6	12.1	11.3	10.6	9.7	9.3	8.9	8.4	8.0
250	14.0	14.2	14.7	13.9	13.5	13.4	12.9	12.8	12.2	11.7	11.1	10.9	10.6	10.0	9.5	8.9	8.5	8.1	7.7	7.4
300	11.5	11.6	12.0	11.8	11.6	11.6	11.2	11.2	10.8	10.5	10.0	9.8	9.6	8.9	8.4	8.0	7.7	7.3	7.2	6.8
400	8.4	8.7	8.8	9.0	9.0	9.0	8.8	8.7	8.6	8.4	7.8	7.6	7.6	7.2	6.7	6.5	6.4	6.2	6.3	6.0
500	6.6	6.6	6.6	6.7	6.8	6.8	6.7	6.7	6.7	6.3	6.1	6.1	6.0	5.9	5.7	5.6	5.5	5.6	5.6	5.4
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614
D I S T A N C E																				

MEAN XBT TEMPERATURE, DEG-C

MID-DECEMBER

0	24.5	24.3	23.8	23.6	23.2	22.9	22.4	22.0	21.5	20.5	20.0	19.6	18.9	18.3	17.4	17.0	16.3	15.5	14.3	12.9
10	24.5	24.3	23.8	23.6	23.2	22.9	22.4	22.0	21.5	20.4	20.0	19.5	18.9	18.3	17.4	17.0	16.3	15.6	14.3	12.9
20	24.5	24.3	23.8	23.6	23.2	22.9	22.4	22.0	21.5	20.4	20.0	19.5	18.9	18.3	17.4	16.9	16.3	15.6	14.3	12.8
30	24.5	24.2	23.8	23.6	23.2	22.9	22.4	22.0	21.5	20.4	20.0	19.6	18.9	18.4	17.5	16.9	16.4	15.7	14.3	12.8
40	24.5	24.3	23.9	23.7	23.2	23.0	22.4	22.0	21.5	20.5	20.1	19.6	19.0	18.5	17.6	16.8	16.5	15.7	14.2	12.5
50	24.5	24.3	23.9	23.6	23.3	23.0	22.5	22.1	21.5	20.5	20.0	19.7	19.1	18.5	17.7	16.9	16.5	15.7	14.1	11.9
D 60	24.6	24.3	23.8	23.6	23.1	22.9	22.6	22.1	21.6	20.5	20.0	19.6	19.1	18.4	17.5	16.4	16.1	15.1	13.4	11.2
E 70	24.6	24.3	23.7	23.5	22.8	22.5	22.5	21.8	21.4	20.2	19.8	19.2	18.6	18.1	16.9	15.5	15.5	14.3	12.5	10.5
F 80	24.2	23.9	23.4	23.1	22.2	22.0	21.9	21.3	20.9	19.6	19.5	18.8	17.9	17.5	16.2	15.0	14.4	13.3	11.6	9.9
T 90	23.5	23.3	23.0	22.5	21.5	21.4	21.0	20.8	20.2	19.1	19.2	18.3	17.4	16.9	15.7	14.2	13.3	12.4	11.0	9.7
H 100	22.9	22.6	22.5	21.9	21.0	20.8	20.2	20.0	19.6	18.5	18.6	17.7	16.9	16.2	15.0	13.7	12.7	11.8	10.6	9.5
120	21.5	21.2	21.2	20.6	20.0	19.6	19.0	18.9	18.4	17.4	17.6	16.9	16.1	15.3	14.3	12.9	11.9	10.9	9.9	9.1
(M) 150	20.1	19.7	19.9	19.2	18.6	18.2	17.8	17.5	17.0	16.1	16.1	15.6	14.7	13.9	12.8	11.5	10.6	9.9	9.2	8.7
200	17.2	17.2	17.6	16.6	16.1	15.8	15.3	15.2	14.4	13.5	13.1	12.7	12.0	11.4	10.5	9.8	9.3	8.9	8.5	8.0
250	13.9	14.1	14.7	13.7	13.4	13.3	12.8	12.6	12.2	11.7	11.1	10.9	10.5	10.0	9.5	8.9	8.5	8.1	7.8	7.4
300	11.4	11.5	12.0	11.7	11.5	11.5	11.2	11.2	10.9	10.5	9.9	9.8	9.5	9.0	8.4	8.0	7.7	7.3	7.2	6.9
400	8.3	8.6	8.8	8.9	8.9	8.9	8.8	8.7	8.6	8.3	7.8	7.7	7.5	7.2	6.7	6.5	6.4	6.2	6.2	6.1
500	6.6	6.6	6.6	6.7	6.9	6.8	6.7	6.6	6.6	6.4	6.2	6.2	5.9	5.8	5.7	5.6	5.5	5.6	5.6	5.5
N MI	50	150	250	350	450	550	650	750	850	950	1050	1150	1250	1350	1450	1550	1650	1750	1850	1950
KM	93	278	463	649	834	1019	1205	1390	1575	1761	1946	2131	2317	2502	2687	2872	3058	3243	3428	3614
D I S T A N C E																				

OCEANIC CONDITIONS DURING 1976 BETWEEN
SAN FRANCISCO AND HONOLULU
AS OBSERVED FROM SHIPS OF OPPORTUNITY

J. F. T. Saur¹ and D. R. McLain²

INTRODUCTION

During 1976 cooperating merchant ships continued to make sections of surface salinity samples and of expendable bathythermograph (XBT) observations on the San Francisco-Honolulu ship route (Fig. 7.1). Similar sections of observations were obtained most of the year, but less frequently, on the Seattle and Los Angeles to Hawaii routes. These, however, were discontinued at the end of October for lack of funds, and these two routes are not considered in this paper. The sampling was done for the National Marine Fisheries Service using funds provided by the National Science Foundation under the NORPAX program.

The San Francisco-Honolulu route crosses a Transition Zone which lies between the cooler, lower salinity, modified subarctic waters of the California Current and the warmer, higher salinity waters of the Eastern North Pacific (ENP). Laurs and Lynn (1975, 1977) indicated that the character and position of the Transition Zone, directly or indirectly, influence the offshore distribution and migration routes of albacore tuna moving from the central North Pacific into the summer fishery off the continental west coast.

Selected vertical sections of the data have been published monthly in Fishing Information³ since March 1972. Interpretations of features in the sections were included through March 1975 (Saur 1972-75). Saur et al. (1979) discussed the characteristics of long-term mean vertical sections of subsurface temperatures from the XBT data on the San Francisco route.

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In this report we present distributions of surface salinity, sea surface temperature (SST), and heat storage (surface to 100-m layer) during 1976, and have extended the previously published 1972-75 time series of their anomalies through 1976. We discuss the 1976 distributions and differences in anomalies from the preceding years. An apparently atypical relation of positive temperature anomalies occurring with negative salinity anomalies off the Pacific coast during October-December 1976 is attributed, at least partially, to a decrease in evaporation and weak vertical mixing by winds.

OBSERVATIONS

Observational programs and procedures for making XBT observations aboard cooperating merchant ships have been described by Saur and Stevens (1972). The "surface" salinities are determined from water samples drawn at around 7 m below the surface. "Surface" temperatures from the XBT observations are representative of temperatures at about 5 m. Heat storage is presented as average temperature from the surface to 100 m as determined from the XBT observations. These observations were normally scheduled at 4-h intervals.

For 1976 the number of ship of opportunity transits, number of observations, and range of observed values are shown in Table 7.1.

Table 7.1

	Number of		Minimum	Maximum	Range
	Transits	Obs.			
Surface salinity (o/oo)	27	814	32.37	35.59	3.22
Surface temp. (C)	31	926	10.0	25.9	15.9
Heat storage (C, 0-100 m)	30	868	10.0	25.2	15.2

The locations of the observations are shown in Figures 7.2-7.4. In these, and other figures, the location of an observation is given by its great circle distance from a reference point, 21N12', 157W42', which is in the ocean channel near Honolulu, south of Makapuu Point, Oahu.

DISTRIBUTION OF VARIABLES DURING 1976

The time-space distributions of salinity, temperature, and heat storage (0-100 m) are shown in Figures 7.2, 7.3, and 7.4, respectively. The irregularly located observations were first analyzed by the NORPAX/SURFACE II computer program to a time-space grid of 24 intervals per year by 92.6 km (50 n mi). The distributions were then computer contoured from the unsmoothed grid fields using double linear interpolation with five subintervals within each standard grid interval.

The surface salinities (Fig. 7.2) showed the underlying mean pattern (Saur 1978) of a low salinity minimum (below 33.0 o/oo) a short distance offshore in the California Current; a region where salinity increased toward Hawaii and had maximum gradients located between 2,000 km and 3,000 km along the route from Hawaii; a region of maximum salinities (above 35.0 o/oo) located between 500 km and 1,750 km from Hawaii; and somewhat lower salinities (below 35.0 o/oo) most of the year near Hawaii. The high salinities occurred where the vessel track crossed the eastern end of the high salinity Eastern North Pacific Central Waters, located between 25N and 30N (Sverdrup et al. 1942).

The surface temperatures (Fig. 7.3) showed the typical annual cooling and warming cycle with minimum temperatures in late March or early April and maximum temperatures in September superimposed on the latitudinal decrease in temperature along the route from Hawaii to San Francisco. The most rapid warming normally occurs from mid-May to mid-July, but in 1976 the warming was delayed until mid-June and was greatest in July. This was followed by a broad maximum through October and slowly decreasing temperatures in November-December.

The annual cycle of temperature is much more prominent than the annual cycle of salinity. Minimum and maximum values and total range for each gridded field are shown in Table 7.1. The greatest range of salinity at a given position was about 0.5 o/oo or only 15% of the total observed range. On the other hand, near the California coast the temperature range was 6.0C, and near 3,000 km along the route (in the Transition Zone) the annual range was 5.1C, which were 39% and 32%, respectively, of the total observed range.

The heat storage (expressed by the average temperature in the upper 100 m of water, Fig. 7.4) had a pattern similar to that of surface temperature. However, at a fixed location it did not have as large an annual range; this was only about 2C over most of the route but reached about 4C near the California coast. The smaller annual range of heat storage occurred because the effects of the seasonal warming and cooling cycle decrease with depth.

ANOMALIES DURING 1976

The time series since 1972 of anomalies of salinity, temperature, and heat storage given by Saur (1978) are extended to include 1976 anomalies (Fig. 7.5). The mean data from which the anomalies were computed did not include the 1976 data, but were for the same 8-yr period (June 1966-December 1970, January 1972-June 1975) used previously. The grid fields for the anomalies were numerically smoothed by a 5 x 3 point (60 days by 100 n mi) before being contoured.

The anomalies of surface salinity were generally small, but dominantly positive, throughout the first nine months of 1976. Two exceptions are noticeable. Along the California coast there was a pulse of below normal salinity water in January-February and another in May-July. Nearer midsection the negative anomaly (-0.2 o/oo) which had appeared near 2,700 km in late summer 1975 migrated westward along the track, decreased to near normal in winter, but then increased in intensity to -0.2 o/oo around 2,000 km in May and June 1976. This propagation speed along the route was about 3.3 cm/s as compared with observed values of 2.5 cm/s in 1972-75 and speeds of 2.9 cm/s for temperature anomalies at 170 m (generally in the thermocline) found by Dorman and Saur (1978).

The outstanding feature of surface salinity anomalies in 1976 was the appearance of significant negative anomalies (below -0.2 o/oo) at the California coast and also near the outer edge of the California Current (near 2,800 km) in October. In mid-November there was a band of negative anomalies (below -0.3 o/oo) from near the California coast to midsection. Further, anomalies below -0.4 o/oo occurred in the Transition Zone and extended toward Hawaii somewhat into the ENP region. These strong negative anomalies appeared to be returning to near normal at the end of the year.

The SST anomalies in 1976 exhibited the earlier observed coherence with distance along the track and low persistence in time. From January through April temperature anomalies were positive over most of the route except that they were negative within about the last 600 km approaching the California coast. A change to significantly negative anomalies occurred in May over the entire route because of the previously mentioned delayed onset of seasonal warming. Warming in July briefly returned the anomalies to near zero over most of the route. A narrow band of positive anomalies appeared near the California coast at that time. The anomalies over the rest of the route returned, however, to significantly negative values during August through October.

During the last quarter, positive temperature anomalies appeared progressively farther westward along the route towards Hawaii at a very rapid rate. Significant positive anomalies (above 0.5C) appeared during November over the entire eastern half of the section and persisted through the remainder of the year. The pattern of these positive anomalies was quite similar to that of the negative salinity anomalies that were previously noted.

The pattern of anomalies of heat storage in the upper 100 m differed considerably from that of surface temperature anomalies. Only during the first quarter of the year was there some correspondence of positive anomalies of heat storage and surface temperature over most of the route along with negative anomalies near the California coast. During May-July over the central portion of the route, the positive anomalies of heat storage persisted while the anomalies of SST changed to negative, indicating that the warm waters remained at depth but were covered with anomalously cool waters at the surface.

Toward the last half of the year negative heat storage anomalies progressively appeared over a larger portion of the route at the Hawaiian end of the section. Otherwise, the patterns of significant heat storage anomalies were very spotty.

DISCUSSION

The oceanic conditions in 1975 on the San Francisco-Honolulu route began with the relation between surface salinity and surface temperature anomalies which has been typical for at least the period 1972-75. This historical relation had banded and westward-migrating positive (or negative) salinity anomalies over the eastern half of the route accompanied by positive (or negative) surface temperature anomalies over most of the route. This relation continued in the first quarter of 1976 when positive salinity anomalies were associated with positive temperature anomalies.

During midyear the relation broke down and 1976 ended with a strongly atypical relation between salinity and temperature anomalies. Negative salinity anomalies occurred simultaneously for 1,500 km along the eastern part of the route with positive temperature anomalies--a reversal from the previous relation.

For the years 1972-75 an heuristic model with anomalies dominated by advective processes could explain the association of positive salinity anomalies in the outer California Current region with wider spread positive temperature anomalies. The California Current is the fastest portion of the eastern limb of the major (clockwise) gyre of the central North Pacific. Along the

San Francisco-Honolulu route the average current flows from northwest to southeast, essentially normal to the route. An increase in speed of the North Pacific Gyre would bring in more cool, low salinity, modified Subarctic Water which, on the route, would appear first in the California Current region and later in the Transition Zone. This would result in more negative salinity and temperature anomalies in these areas. Over the western half of the route, an increase in speed of the gyre would also result in increasingly negative temperature anomalies (due to meridional gradients of temperature) but would not result in significant negative salinity anomalies because meridional salinity gradients are weak or nonexistent in that area (Reid 1969). The increase (or decrease) in speed of the gyre could result from long-term forcing by winds. This simple model assumes that the variability from heat exchange and vertical mixing is negligible.

The patterns of salinity and temperature diverged greatly from this model in the last three months of 1976. Dickson and Namias (Paper 2) noted that during 1976 the upper air (700 mb) patterns also changed noticeably. During the first three seasons the anomalous circulation was strongly zonal across the central North Pacific. But during the last three months, a high pressure ridge established itself over the eastern North Pacific and west coast of North America. The ensuing fair weather and 1976-77 winter drought over the western United States were documented in the Monthly Weather Review.⁴

The breakdown in October through December 1976 of the earlier relation between salinity and temperature anomalies indicated a change in balance of oceanic processes. If we consider that surface salinity is a quasi-conservative property and the low anomalies were due to increased advection to the south, we must look for processes that would change a negative temperature anomaly to positive. The possibility that increased anomalous heat exchange and less vertical mixing by weaker winds contributed to positive anomalies was explored using monthly mean data compiled by 5-deg quadrangles at the Southwest Fisheries Center. Anomalies were computed for two quadrangles for the last three months of 1974, 1975, and 1976 (Table 7.2). One of the quadrangles (35N-40N, 125W-130W) lies over the California Current west of San Francisco and is crossed by the ship route. The other (40N-45N, 125N-130W) is the adjacent quadrangle to the north, through which waters normally flow before crossing the route. Heat exchange anomalies were computed from the 1961-71 means given by Clark et al. (1974). Wind speed anomalies were computed from the 1961-76 monthly means published in 1976 issues

⁴Professional journal of the American Meteorological Society, Vol. 105, Nos. 2-5, February-May 1977.

of Fishing Information.

The anomalies showed that wind speeds were lower and heat gained by the ocean was much higher in 1976 than in the previous two years. The decreased wind speeds along with occurrence of warm, moist air resulted in less evaporation and sensible heat loss and, consequently, more heat retention by the ocean (Table 7.2). Decreased wind speeds also permitted more stratification in the ocean and thus a greater positive surface temperature anomaly from the excess heat gain.

The major characteristics of anomalies which stand out in Table 7.2 are:

- 1) In both quadrangles there was a month to month consistency of heat exchange anomalies in 1976, particularly as compared with 1974. The same consistency occurred in the anomalies of wind speed.
- 2) Above normal retention of heat by the ocean because of reduced evaporation was the major component in 1976. Above normal incoming radiation and lower flux of sensible heat were secondary terms. Year to year changes of effective back radiation were relatively small.
- 3) The total heat flux anomaly in 1976, the anomaly from decreased evaporation, and the wind speed anomaly were larger in magnitude in the area to the north of the route (upcurrent) than in the immediate area of the XBT observations.

The data presented in Table 7.2 indicated that processes (heat exchange and vertical mixing) previously considered small as compared with advective processes were, at least partially, responsible for the late 1976 reversal of the relation of salinity anomalies to temperature anomalies observed in 1972-75. We are mindful that this argument is based on the assumption that the salinity anomalies resulted from advection and that the temperature anomalies were atypical. It is not immediately apparent how one could interpret the data if the temperature anomalies were assumed to be advective and it were necessary to explain the salinity anomalies as atypical.

ACKNOWLEDGMENTS

We thank the Chevron Shipping Co. and Matson Navigation Co. for their cooperation and that of their ships' personnel in making the observations used herein. The Fleet Numerical Weather Central supplied the XBT probes and the use of computer facilities at Monterey.

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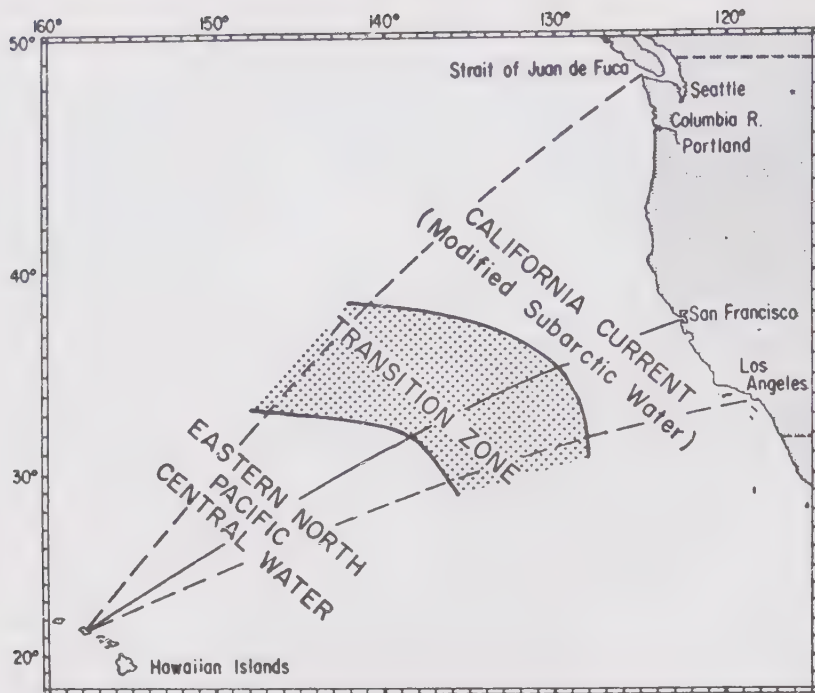


Figure 7.1.—Three oceanic domains (schematic) in the eastern North Pacific Ocean crossed by cooperating merchant ships taking surface salinity and expendable bathythermograph observations during 1976. Observations reported herein were taken on the San Francisco to Honolulu route (solid line).

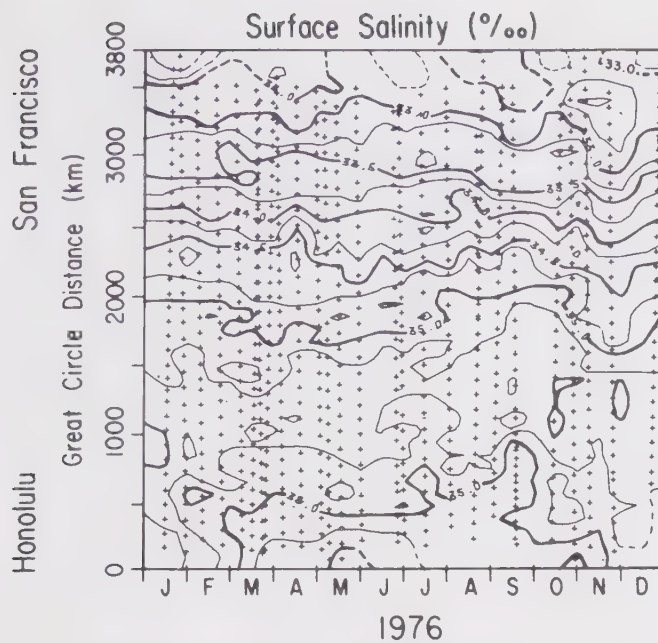


Figure 7.2.—Surface salinity in parts per thousand (‰) between San Francisco and Honolulu during 1976. Symbols (+) indicate the locations of observations in time and distance. Contour interval is 0.25‰.

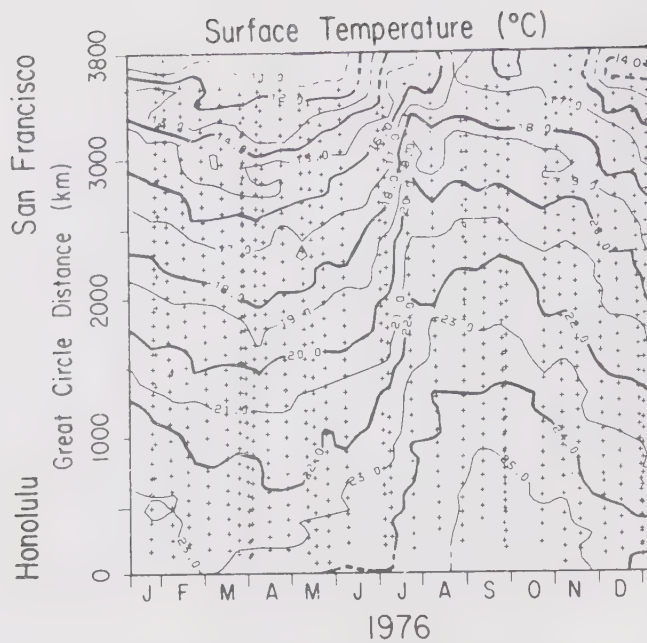


Figure 7.3.—Sea surface temperature in degrees Celsius (C) between San Francisco and Honolulu during 1976. Symbols (+) indicate the locations of observations in time and distance. Contour interval is 1.0C.

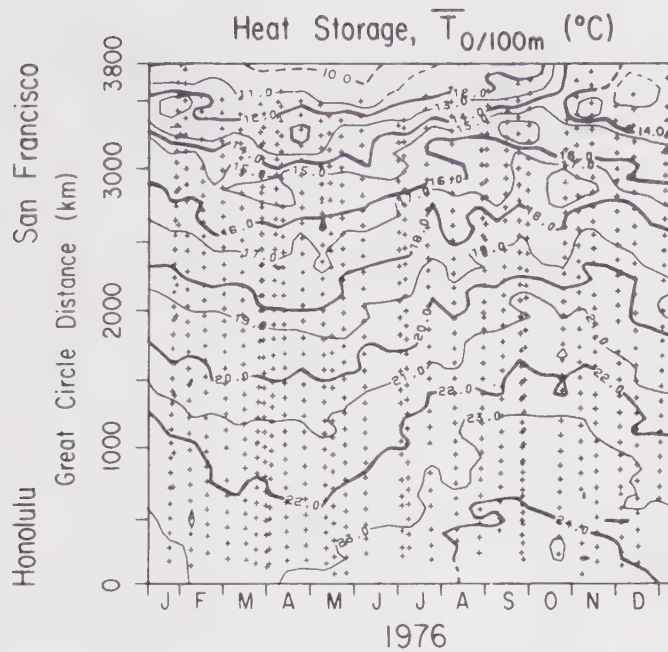
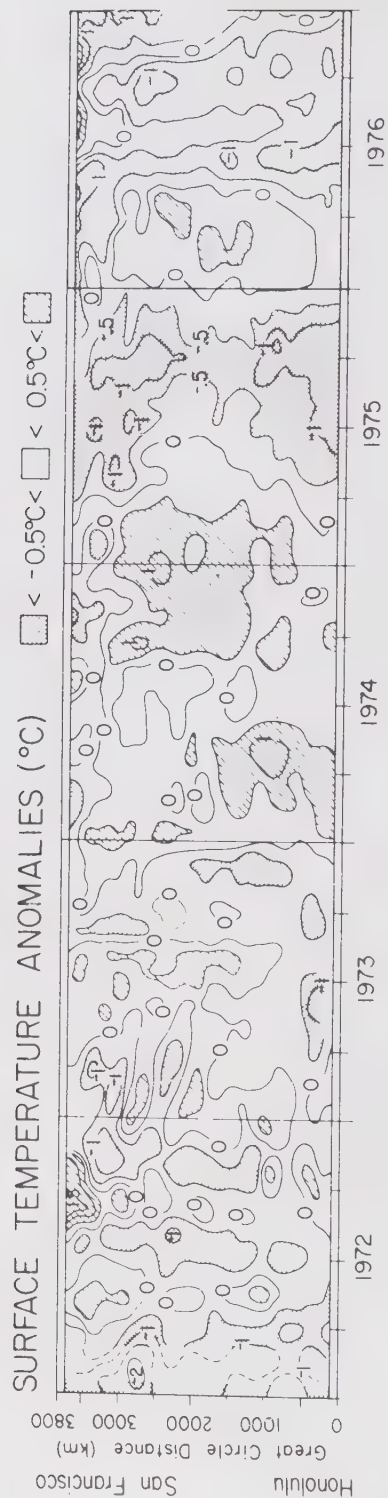
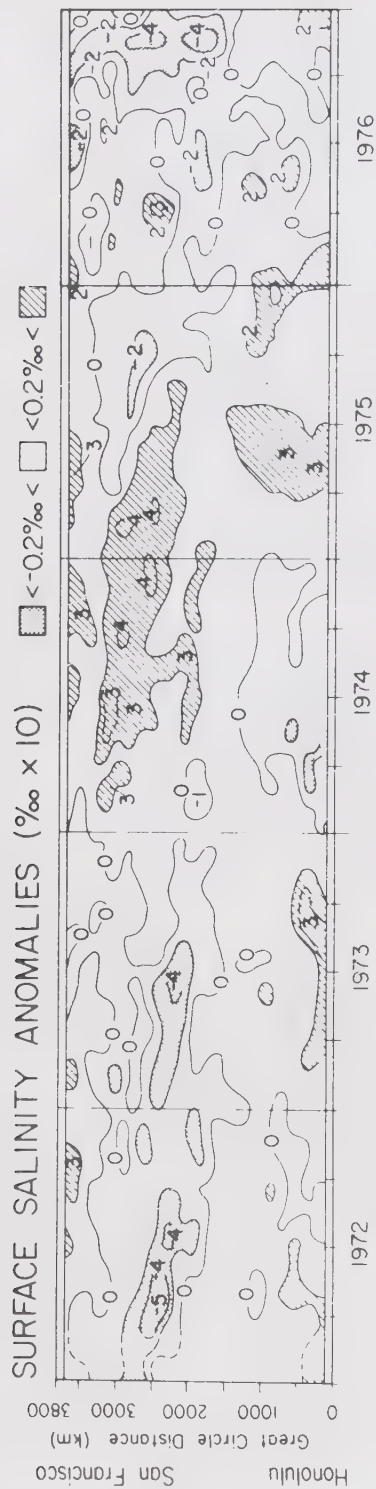


Figure 7.4.—Heat storage for the surface to 100-m layer, expressed as average temperature ($\overline{T}$) 0-100 m in degrees Celsius ($^{\circ}\text{C}$), between San Francisco and Honolulu during 1976. Symbols (+) indicate the locations of the expendable bathythermograph observations. Contour interval is 1.0°C .



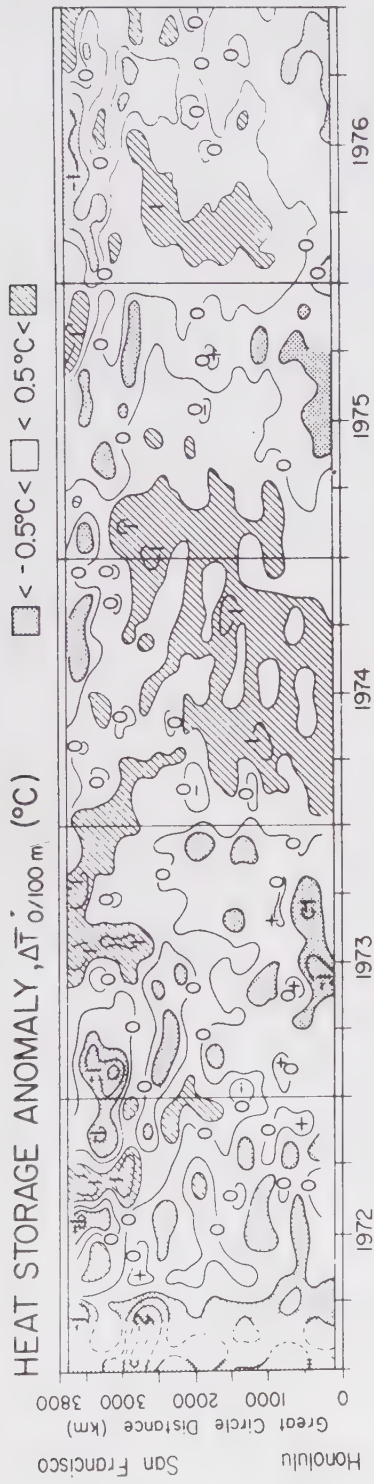


Figure 7.5.—Anomalies on the San Francisco-Honolulu route, January 1972–December 1976. Analyses in all three panels were smoothed before contouring (see text). Upper: Salinity anomalies; labels on contours are the anomaly multiplied by 10. Center: Sea surface temperature anomalies; contour interval is 0.5°C. Lower: Heat storage anomalies for the surface to 100-m layer, expressed as departure from the mean of average temperature (T) 0–100 m in degrees Celsius.

TABLE 7.2. Anomalies of heat exchange ($\text{cal cm}^{-2} \text{ d}^{-1}$) and of wind speed (knots) at two 5-degree quadrangles in the California Current Region. Quadrangles lie a) on San Francisco to Honolulu ship route and b) upcurrent from route. Positive (negative) values indicate anomalous heat gain (loss) by the ocean.

	1974			3-mo mean	1975			3-mo mean	1976			3-mo mean
	Oct	Nov	Dec		Oct	Nov	Dec		Oct	Nov	Dec	
On route (lat. 35°-40°N, long. 125°-130°W):												
Incoming radiation	19	-4	9	8	-12	3	-18	-9	7	3	23	11
Effective back radiation	-10	-6	1	-5	7	-7	19	6	-3	-6	-10	-6
Evaporation	-3	-58	26	-12	-18	-40	54	-1	13	19	17	16
Sensible heat flux	-4	-16	13	-2	10	-4	14	7	1	-3	11	3
Total (net) heat flux	2	-84	49	-11	-13	-48	69	3	18	13	39	23
Wind speed (knots) anomaly	-1	-2	0	-1	1	1	-1	0.3	-3	-3	-2	-2.7
Upcurrent from route (lat. 40°-45°N, long. 125°-130°W):												
Incoming radiation	-3	-10	4	-3	-20	11	-10	-6	20	15	17	17
Effective back radiation	13	-9	6	3	18	-3	16	10	1	-2	-5	-2
Evaporation	57	-73	39	8	8	22	60	30	44	35	61	47
Sensible heat flux	17	-31	26	4	21	12	15	16	18	15	24	19
Total (net) heat flux	84	-122	76	13	26	43	81	50	82	63	97	80
Wind speed (knots) anomaly	-1	4	-1	0.7	4	2	-1	1.7	-2	-3	-5	-3.3

MERCURY AND SELENIUM IN
BLUE MARLIN, *MAKAIRA NIGRICANS*,
FROM THE HAWAIIAN ISLANDS

In a previous study, nine species of pelagic and inshore fish caught in Hawaiian waters were analyzed for total and organic mercury (Rivers et al. 1972). In all but one species the organic mercury was >80% of the total, a finding consistent with other mercury values reported (Kamps et al. 1972; Westöo 1973). In muscle and liver tissues of blue marlin, *Makaira nigricans* Lacépède, however, only a small portion of the total mercury was found to be organic mercury. Additional studies on marlin landed during fishing tournaments in 1972 (Schultz et al. 1976) and 1973 (Schultz and Crear 1976) revealed low levels of organic mercury in six other tissues. These studies also showed that the difference between total and organic mercury was indeed inorganic mercury. G. Westöo (National Swedish Food Administration, Stockholm. Pers. commun., 1972) had previously identified the organic fraction as methyl mercury.

An assessment of mercury is complicated by the presence of selenium. Selenium has been shown to reduce the toxicity of mercuric chloride and methyl mercury in laboratory animals when given as selenite, selenomethionine, or as selenium present in tuna (Pařízek et al. 1971; Ganther and Sunde 1974). The presence of selenium in tuna, a principal food item of marlin (Naughton¹), indicates that it should also be present in marlin.

For this report, nine tissues from blue marlin were analyzed for selenium, total mercury, and organic mercury.

Materials and Methods

Samples of muscle, liver, kidney, spleen, pyloric caecum, stomach, gill, gonad, and blood were collected from 46 marlin landed during a fishing tournament in Kailua-Kona, Hawaii, during August 1974. The tissues were ground with Dry Ice² in a blender and stored in acid-washed plastic vials.

The organic extraction was carried out as described by Rivers et al. (1972), i.e., a benzene extraction of the methyl mercury was reextracted with cysteine, oxidized with permanganate, and reduced to elemental mercury with stannous ion prior to being volatilized into the flameless atomic absorption apparatus. Total mercury digestions were performed (Rivers et al. 1972) but with 10 ml of concentrated nitric acid instead of 30 ml. All analyses were made with a Perkin-Elmer 303 atomic absorption spectrophotometer equipped with a vapor chamber (Manning 1970).

Selenium was determined by a fluorometric technique (Watkinson 1966), as modified by S. Nishigake (Tokyo Metropolitan Research Laboratory of Public Health, Tokyo, Japan. Pers. commun., 1975), i.e., following sample digestion with nitric and perchloric acids, the selenium was complexed with 2,3-diaminonaphthalene and this fluorescent compound then extracted into cyclohexane. All analyses were made using a Turner Model 110 fluorometer equipped with a primary filter at 369 nm and a secondary filter at 522 nm.

¹Naughton, J. J. 1973. To all billfishermen. (Summary report of 15th Hawaiian International Billfish Tournament, 27-31 August 1973), 9 p. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

A summary of mercury and selenium concentrations in the marlin is given in Table 1. Average total mercury and selenium values were greatest in kidney (26.33 mg/kg Hg, 23.42 mg/kg Se) and least in blood (0.18 mg/kg Hg, 1.29 mg/kg Se) and gill (0.32 mg/kg Hg, 1.29 mg/kg Se). Average methyl mercury was highest in muscle (0.40 mg/kg) and lowest in blood (0.04 mg/kg) and gill (0.06 mg/kg). The percentage of organic to total mercury ranged from 1% in kidney to 27% in gonad. The molar ratio of mercury to selenium ranged from 0.06 in blood to 0.62 in muscle. (Molar ratio is computed here using sample average statistics of combined male and female data.)

An analysis of variance revealed significant differences ($P < 0.05$) in total mercury between males and females for all tissues except gill and blood. A similar pattern was found for selenium. The organic mercury levels were not statistically different ($P > 0.05$) between the sexes. In earlier studies on marlin caught from the same area during fishing tournaments in 1971, 1972, and 1973, mercury concentrations in both sexes were found to be similar.

Table 2 presents correlation coefficients for body weight and tissues. In most cases, the relationships are positive and highly significant. Figures 1-6 illustrate the dependence of mercury and selenium on weight and on each other.

Discussion

The data clearly demonstrate that methyl mercury concentrations are low relative to total mercury in blue marlin. Westöo (pers. commun.) and Nishigaki (pers. commun.) confirmed this low percentage in our samples based on subsamples sent to them. Nishigaki has also confirmed our selenium results.

In a study of 37 Pacific blue marlin (50-238 kg, average 109 kg) from Japanese waters, Nishigaki (pers. commun.) found total mercury levels ranging from 0.02 to 13.0 mg/kg (average 2.83 mg/kg) and methyl mercury ranging from 0.02 to 1.28 mg/kg (average 0.57 mg/kg). Selenium values for 11 marlin ranged from 0.52 to 1.99 mg/kg, averaging 0.97 mg/kg. These values are similar to our findings for mercury and selenium in marlin from Hawaiian waters.

TABLE 1.—Summary of mercury and selenium data in 46 blue marlin from the Hawaiian Islands by sex.¹

Tissue	Total Hg (mg/kg)				Organic Hg (mg/kg)				% organic Hg of total Hg	Se (mg/kg)				Hg/Se molar ratio
	Mean		Range		Mean		Range			Mean		Range		
	M & F	M	F	M & F	M & F	M	F	M & F		M & F	M	F	M & F	M & F
Muscle	3.12	2.83	3.76	0.09-10.00	0.40	0.32	0.58	0.02-1.02	13	1.98	1.88	2.21	0.63-5.32	0.62
Liver	11.58	12.53	9.46	0.13-39.20	0.26	0.21	0.38	0.09-0.76	2	17.47	20.36	11.06	2.50-61.12	0.26
Kidney	26.33	26.25	26.53	0.18-77.00	0.22	0.16	0.35	0.04-0.86	1	23.42	25.33	19.06	2.63-56.25	0.44
Spleen	6.93	6.34	8.21	0.08-17.60	0.18	0.12	0.30	0.02-0.66	3	9.31	9.12	9.73	0.63-24.25	0.29
Stomach	1.27	1.33	1.16	0.06-3.00	0.12	0.08	0.21	0.03-0.47	9	2.91	3.16	2.39	1.35-4.03	0.17
Pyloric caecum	1.83	1.74	2.03	0.17-4.50	0.30	0.22	0.49	0.08-0.98	16	4.92	5.10	4.52	2.28-10.10	0.15
Gill	0.32	0.26	0.44	0.08-0.96	0.06	0.03	0.11	0.01-0.34	19	1.29	1.31	1.26	0.71-2.21	0.10
Gonad	0.40	0.30	0.68	0.03-2.15	0.11	0.06	0.25	0.03-0.65	27	2.14	1.97	2.60	1.24-3.80	0.07
Blood	0.18	0.18	0.18	0.02-0.53	0.04	0.04	0.05	0.01-0.11	22	1.29	1.33	1.19	0.72-2.30	0.06

¹Weights of 32 males ranged from 58 to 112 kg (average 80); 14 females weighed 39, 75, and 115-342 kg (average 166). Average for all samples was 106 kg.

TABLE 2.—Correlation coefficient of mercury, selenium, and weight in 46 blue marlin from the Hawaiian Islands by sex.

Tissue	Total Hg:wt			Organic Hg:wt		Organic total Hg		Se wt		Total Hg:Se		Organic Hg:Se	
	M & F	M	F	M & F	M & F	M & F	M & F	M	F	M & F	M & F	M & F	M & F
Muscle	0.69**	0.90**	0.83**	0.79**	0.72**	0.68**	0.88**	0.85**	0.93**	0.61**	0.08	0.61**	0.08
Liver	0.23	0.76**	0.69**	0.76**	0.13	0.00	0.68**	0.38	0.80**	0.80**	0.30*	0.80**	0.30*
Kidney	0.49**	0.83**	0.79**	0.87**	0.42**	0.32*	0.79**	0.73**	0.91**	0.91**	0.41**	0.91**	0.41**
Spleen	0.61**	0.88**	0.75**	0.84**	0.51**	0.45**	0.72**	0.61*	0.87**	0.87**	0.41**	0.87**	0.41**
Stomach	0.38*	0.77**	0.82**	0.81**	0.35*	-0.27	0.18	0.15	0.32*	-0.33*	0.09	-0.33*	0.09
Pyloric caecum	0.59**	0.83**	0.82**	0.86**	0.59**	-0.11	0.32	0.10	0.25	-0.14	0.09	-0.14	0.09
Gill	0.86**	0.70**	0.90**	0.88**	0.77**	0.04	0.08	0.16	0.21	-0.14	0.09	-0.14	0.09
Gonad	0.85**	0.75**	0.95**	0.82**	0.76**	0.15	0.10	-0.53	0.10	0.25	0.09	0.25	0.09
Blood	0.28	0.32	0.57*	0.36*	0.44**	-0.04	-0.17	0.49	0.44**	0.09	0.09	0.44**	0.09

* $P < 0.05$.

** $P < 0.01$.

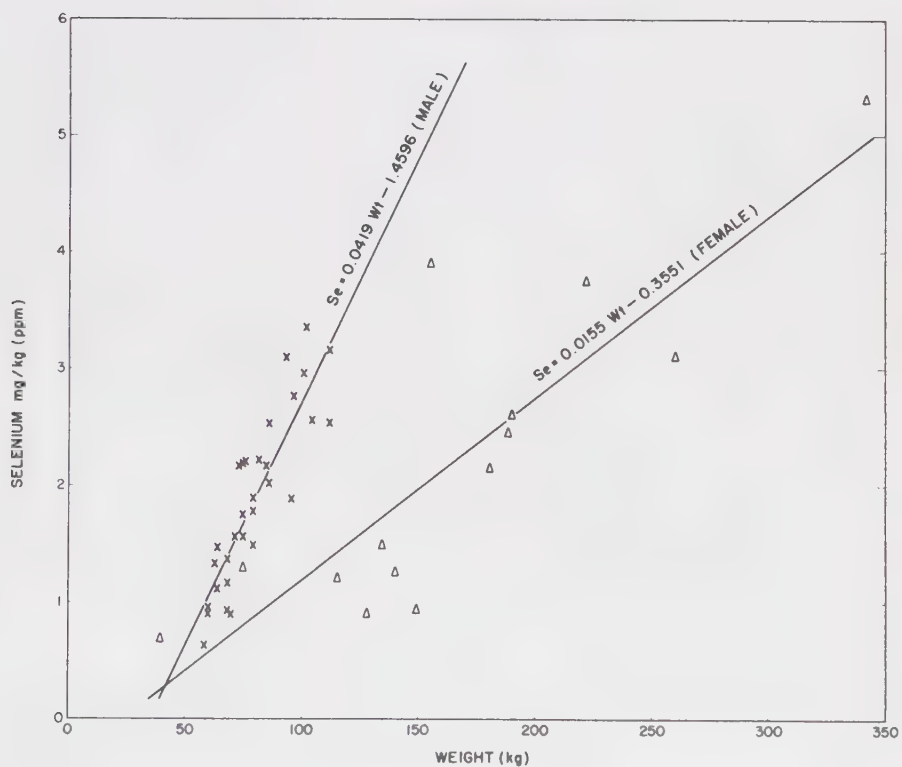
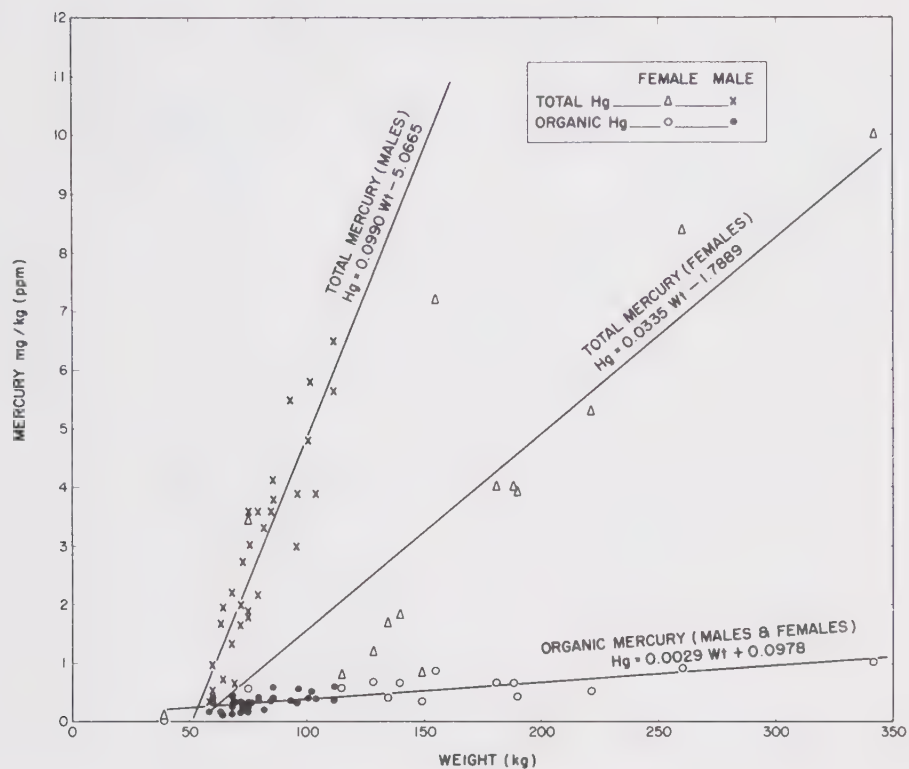


FIGURE 1.—The relationship of total and organic mercury in muscle tissue of 46 blue marlin from the Hawaiian Islands to fish weight.

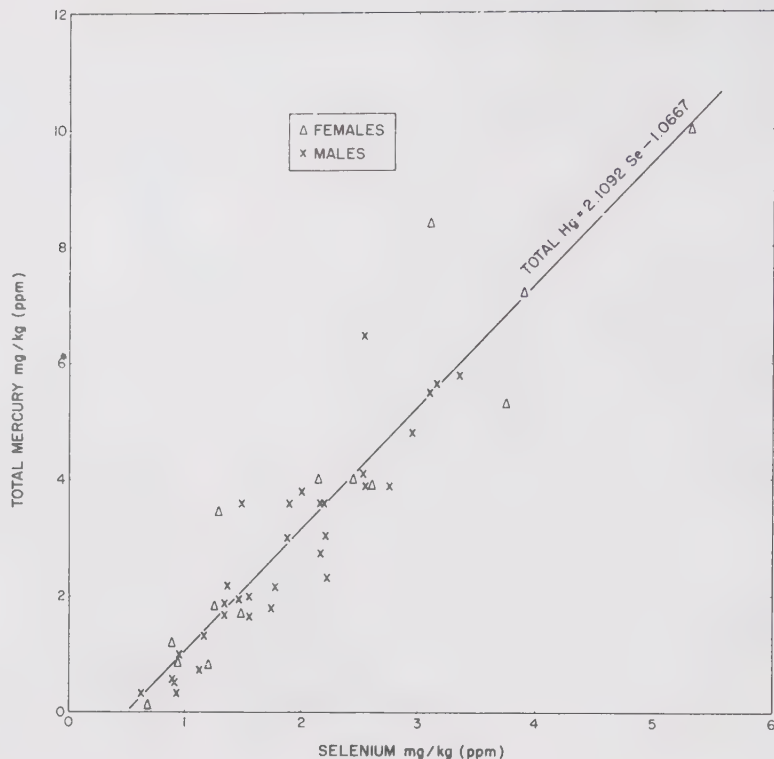


FIGURE 3.—Relationship between total mercury and selenium in muscle tissue of 46 blue marlin from the Hawaiian Islands.

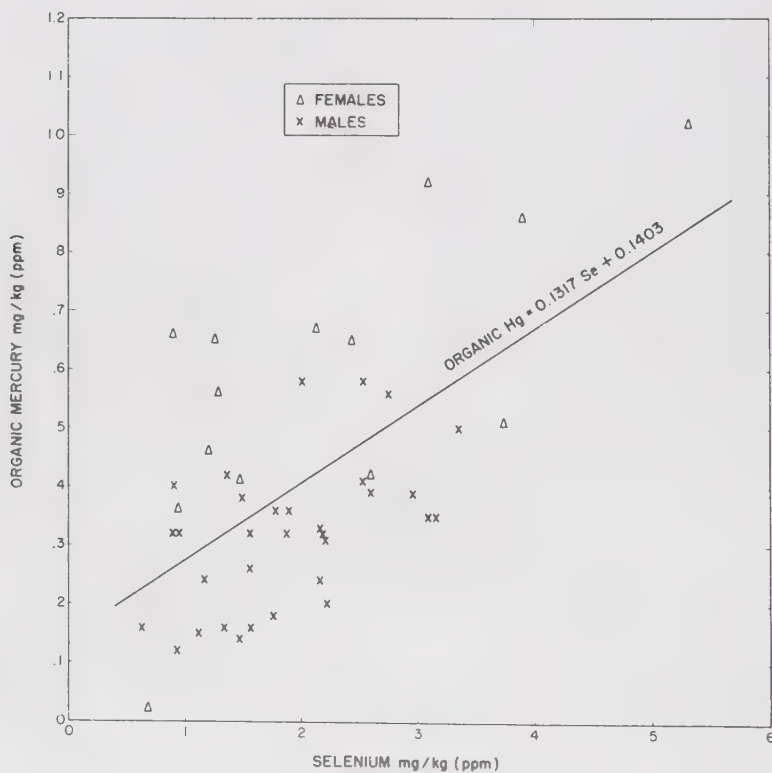


FIGURE 2.—Relationship between selenium in muscle tissue and weight of 46 blue marlin from the Hawaiian Islands.

FIGURE 4.—Relationship between organic mercury and selenium in muscle tissue of 46 blue marlin from the Hawaiian Islands.

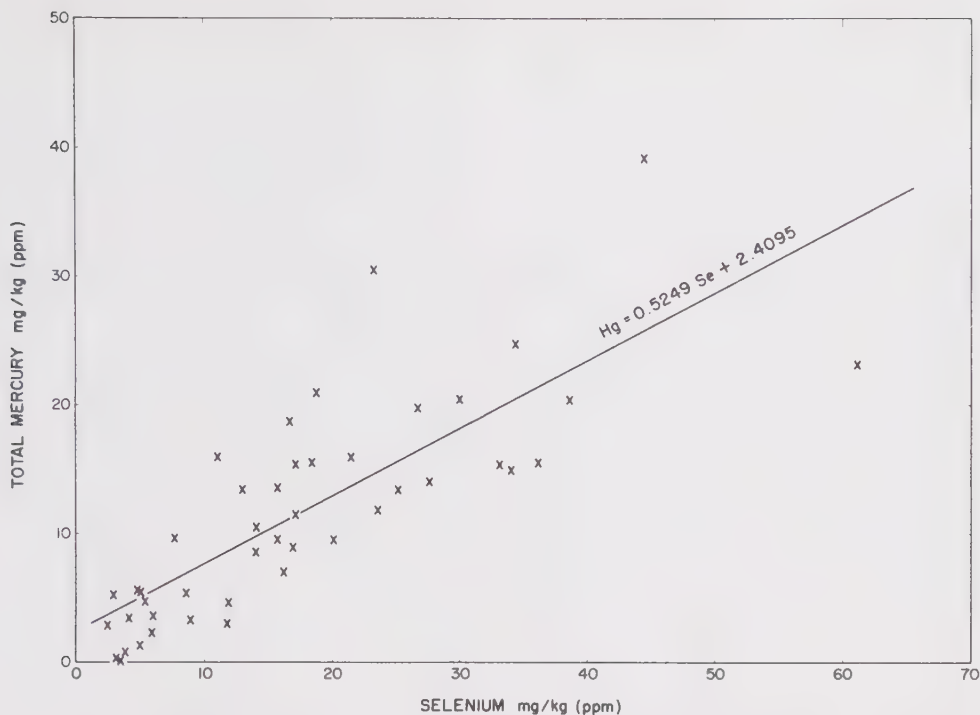


FIGURE 5.—Relationship between total mercury and selenium in liver of 46 blue marlin from the Hawaiian Islands.

Concentration through the food chain is apparently the reason for the elevated levels of mercury found in the marlin. Stomach contents examined in 76 blue marlin captured in 1973 showed that the most common food items were tuna, mostly *Katsuwonus pelamis* (38% occurrence); mackerel scad, *Decapterus pinnulatus* (36%); squid (21%); spiny puffer, *Diodontidae* (19%); and dolphin, *Coryphaenidae* (12%) according to Naughton (see footnote 1).

Mercury levels were reported for yellowfin tuna, *Thunnus albacares*, 0.54 mg/kg; skipjack tuna, *K. pelamis*, 0.38 mg/kg; and for dolphin, *Coryphaena hippurus*, 0.25 mg/kg; by Rivers et al. (1972). These are pelagic species and as such, are exposed to the same amount of mercury in their physical environment; yet all have mercury levels nearly an order of magnitude less than that of the marlin. In addition, their mercury content was essentially all methyl mercury.

If most of the mercury entered the marlin via the food chain as methyl mercury it would seem that demethylation to inorganic mercury had occurred. Conversion of methyl mercury to inorganic mercury has been shown to occur in bluegill

(Burrows and Krenkel 1973) and in rats (Norseth and Clarkson 1970).

It is indicated in Figure 1 that the mercury is accumulated with size but at different rates for males and females. This observation contrasts with previous year's results in which no sex-related concentration disparities were found (Shultz and Crear 1976; Shultz et al. 1976). The reason for this year's anomaly is unclear and not enough information is available to determine if we are dealing with more than one population.

Selenium levels in the marlin are presented in Table 1 and show an increase with weight and age (Figure 2). The high correlation of mercury and selenium with weight (Table 2), and the observation that selenium modifies the activity of mercury in experimental animals, indicate that they are highly correlated with each other, as is seen in Figures 3-6. The precise nature of the mercury-selenium interaction is not known, although a number of suggestions have been advanced. Pařizek et al. (1971) demonstrated with rats that the protective effect of selenite against mercuric chloride was not related to an increase in mercury excretion but to a decrease, resulting in a change

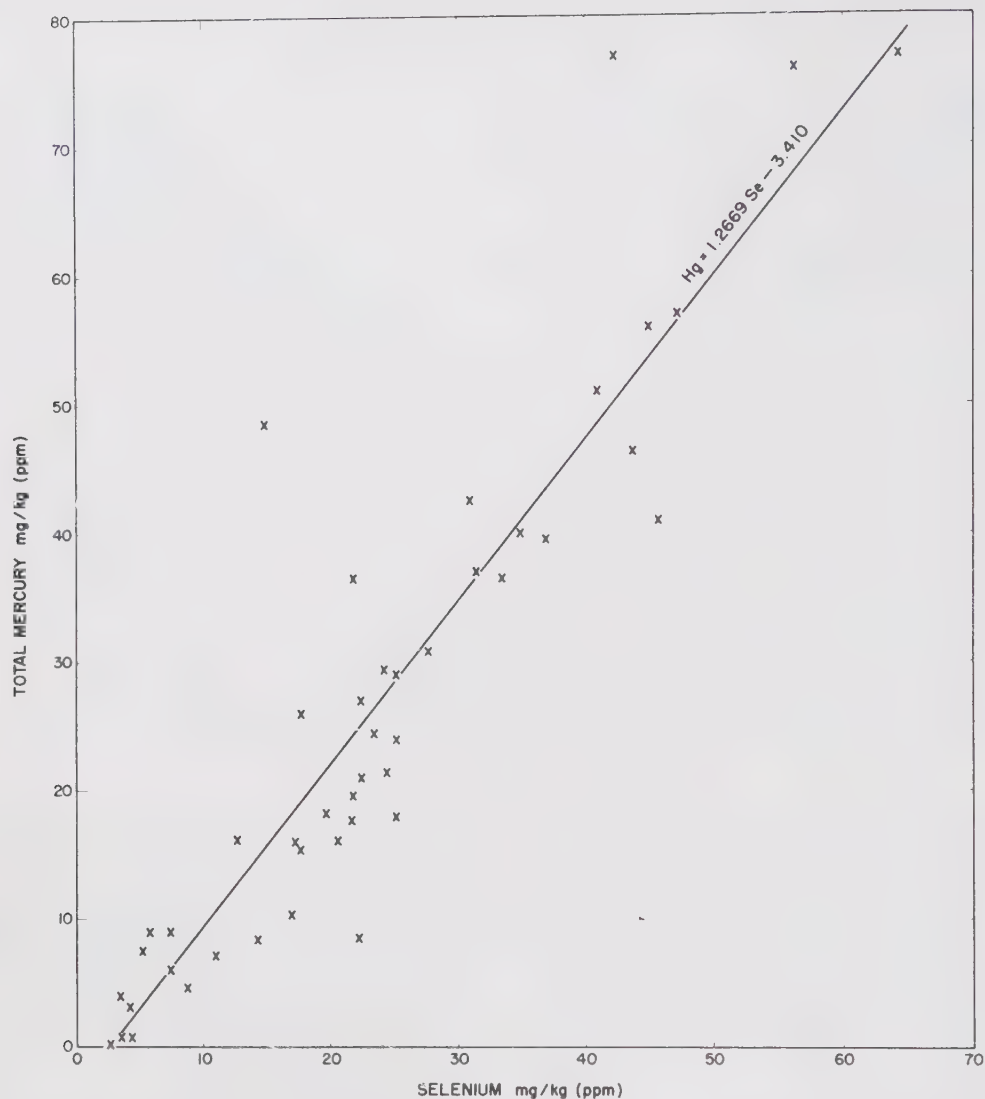


FIGURE 6.—Relationship between total mercury and selenium in kidney of 46 blue marlin from the Hawaiian Islands.

in organ distribution of mercury. The kidneys and intestines lost mercury while the testes gained mercury relative to the controls. In addition, mercury in the macromolecular fraction of blood plasma increased after addition of selenite. Burk et al. (1974) found a similar increase of mercury in plasma protein when mercuric chloride was administered simultaneously with selenite. This was not the case when mercuric chloride or selenite was injected alone. Their experiments using dialysis of rat plasma protein indicated that selenium and mercury are bound in a 1:1 molar

ratio to a single protein, with selenium attached to the protein through a sulfhydryl group and mercury attached to the selenium. They also observed a time lag after injection of selenite before detection of protein binding during which the selenite was apparently metabolized to another form. Lunde (1970) has found selenium to be associated also with proteins in marine organisms.

The molar ratio of average total mercury to average selenium in muscle is 0.62. Subtracting the methyl mercury to obtain inorganic mercury (Schultz and Crear 1976), the ratio reduces to 0.54.

Ganther et al. (1972) reported that the mercury to selenium molar ratio for high-mercury tuna (can tuna) (average 2.87 mg/kg) approaches 0.5. They also noted that the mercury and selenium increments between low-mercury tuna (0.32 mg/kg) and high-mercury tuna were about in a 1:1 molar ratio, implying they are accumulated together.

The total mercury-selenium relationships observed in marine mammals and man are similar to those found in tuna. Koeman et al. (1973) found a 1:1 molar ratio in the livers of seals, *Phoca vitulina*, porpoises, *Phocoena phocoena*, and dolphins, *Tursiops truncatus*, *Delphinus delphis*, *Lagenorhynchus obscurus*, and *Sotalia guianensis*. Regression analyses of their data give an average slope of 2.7 ± 0.2 or 1.1 ± 0.1 on a molar basis for mercury-selenium interactions ($r = 0.932$). Interestingly, they found that only 2 to 14% of mercury in the liver and 2 to 13% in the brain was recovered as methyl mercury. Post-mortem studies on humans exposed to high inorganic mercury (from a mercury mine) showed a 1:1 molar ratio of mercury to selenium ($r = 0.998$) in tissues which had accumulated high amounts of mercury, i.e., thyroid, pituitary, kidney, and brain (Kosta et al. 1975). They noted, however, that this ratio did not exist for a nonexposed group in which mercury and selenium levels were insignificant. Elevated mercury levels were apparently responsible for increasing the selenium concentrations such that, in many cases, the molar ratio of mercury to selenium increments over normal levels approached 1:1 (selenium was low in the mine environment: 1 mg/kg versus 100 mg/kg Hg—in contrast to the relative enrichment of selenium in the diet of tuna and marine mammals). The levels of methyl mercury in organs of the exposed group were low, implying that no significant in vivo methylation occurs in man.

Because selenium is high in the marlin (average 1.98 mg/kg in muscle, 17.47 mg/kg in liver, 23.42 mg/kg in kidney), the possibility of selenium toxicity should not be discounted. Aptly, though, mercury has been shown to mitigate the toxicity of selenium in rats and chicks (Pařízek et al. 1971; Hill 1974).

In an earlier study, it was indicated that cooking did not remove either methyl or total mercury from marlin filets (Schultz and Crear 1976). Higgs et al. (1972) have found that baking does not remove selenium from flounder or chicken although some loss was reported from boiling two

vegetables. It does appear then that mercury (muscle average 3.12 mg/kg) and selenium (muscle average 1.98 mg/kg) concentrations in raw fillet are representative of that in cooked fish.

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SELECTED BIBLIOGRAPHY ON PELAGIC FISH EGG AND LARVA SURVEYS

BIBLIOGRAPHIE SELECTIVE SUR LES PROSPECTIONS D'OEUFs ET DE LARVES DE POISSONS PELAGIQUES

BIBLIOGRAFIA SELECCIONADA SOBRE RECONOCIMIENTOS DE HUEVOS Y LARVAS DE PECES PELAGICOS

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS

ORGANISATION DES NATIONS UNIES POUR L'ALIMENTATION ET L'AGRICULTURE

ORGANIZACION DE LAS NACIONES UNIDAS PARA LA AGRICULTURA Y LA ALIMENTACION

Rome, July 1979

Rome, juillet 1979

Roma, julio 1979

1. SCOPE, COVERAGE AND ORGANIZATION

This bibliography is intended to provide access to published information on ichthyo-plankton survey methods, identification of fish eggs and larvae, and results of surveys that have been carried out in the past. Although the bibliography is selective, its coverage includes all published works through 1973, and it has been extended by the addition of all papers presented at the Oban Symposium and published in the symposium proceedings (Blaxter, J.H.S. (ed.) 1974. The early life history of fish. Springer-Verlag, Berlin).

The first five sections of this bibliography list works by name and date only according to subject category. Section 2 contains references on survey equipment and methods. Section 3 includes descriptions of early life stages organized by taxonomic group. Section 4 lists references on species identification of fish eggs and larvae by region (specifically, by FAO statistical area). Section 5 has reports of survey results, also by region. The bibliography itself, with full citations, is Section 6.

1. PORTEE, CHAMP D'APPLICATION ET ORGANISATION

Cette bibliographie a pour objet d'ouvrir l'accès à l'information publiée touchant les méthodes de prospection d'ichtyoplancton, l'identification des oeufs et des larves de poisson et les résultats des études qui ont été faites dans le passé. Bien qu'elle soit sélective, son champ d'application inclut tous les travaux publiés jusqu'en 1974, et on l'a élargi par l'adjonction de tous les documents soumis au Symposium d'Oban et publiés dans le rapport de ce symposium (Blaxter, J.H.S. (ed.) 1974. The early life history of fish. Springer-Verlag, Berlin).

Dans les cinq premières sections de cette bibliographie sont énumérés des travaux dont on indique le nom et la date, avec ventilation par catégorie de sujets. La Section 2 contient des références sur les méthodes suivies et l'équipement utilisé pour les prospections. La Section 3 inclut des descriptions des stades biologiques initiaux classés par groupe taxonomique. La Section 4 comporte des listes de références sur l'identification des espèces d'oeufs et de larves par région (plus précisément, par zone statistique de la FAO). A la Section 5 figurent des rapports donnant les résultats des prospections, eux-mêmes par région. La bibliographie elle-même, assortie de citations complètes, se trouve à la Section 6.

1. FINALIDAD, ALCANCE Y ESTRUCTURACIÓN

Esta bibliografía se propone facilitar el acceso a la información publicada sobre métodos de reconocimiento ictioplanctónico, identificación de huevos y larvas de peces, y resultados de reconocimientos efectuados en el pasado. Aunque se trata de una bibliografía selectiva, se han incluido todas las obras publicadas hasta 1973, añadiendo además los documentos presentados al simposio de Oban y publicados en las actas del mismo (Blaxter, J.H.S. (ed.) 1974. The early life history of fish. Springer-Verlag, Berlin).

En las cinco primeras secciones de esta bibliografía se indica sólo el autor y la fecha de las publicaciones, agrupadas por temas. La Sección 2 reúne los trabajos sobre equipo y métodos de reconocimiento. La Sección 3 presenta las descripciones de las primeras fases vitales ordenadas por grupos taxonómicos. En la Sección 4 figuran las publicaciones que se ocupan de identificación de especies de huevos y larvas de peces, por regiones (áreas estadísticas de la FAO). La Sección 5 incluye los informes publicados sobre resultados de reconocimientos, también por regiones. La bibliografía propiamente dicha, con citas bibliográficas completas, constituye la Sección 6.

The following specialists have kindly collaborated in the compilation of this selected bibliography, each for the region he or she is most familiar with:

Les spécialistes dont les noms suivent ont collaboré à la préparation de cette bibliographie sélective, chacun d'entre eux pour la région avec laquelle il est particulièrement familiarisé:

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Western Central Atlantic/Atlantique centre-ouest/Atlántico Centro-occidental: C.R. FUTCH (Marine Research Laboratory, St. Petersburg, Florida, U.S.A.)

Indian Ocean Coastal Waters/Eaux côtières de l'océan Indien/Aguas costeras del océano Indico: W. NELLEN (Institut für Meereskunde, Kiel, F.R.G.)

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3. REFERENCES ON SPECIES IDENTIFICATION OF EGGS AND LARVAE, GROUPED TAXONOMICALLY/REFERENCES
 SUR L'IDENTIFICATION DES ESPECES D'OEUF ET DE LARVES, GROUPEES SELON DES CRITERES
 TAXONOMIQUES/BIBLIOGRAFIA SOBRE IDENTIFICACION DE ESPECIES DE HUEVOS Y LARVAS, POR GRUPOS
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3.2.1 Elopidae

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3.2.2 Albulidae

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3.3 Clupeiformes

3.3.1 Clupeidae

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3.3.2 Clupeidae - Engraulidae

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3.3.3 Engraulidae

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3.4 Salmoniformes

3.4.1 Argentinoidei (Argentinidae, Bathylagidae, Opisthoproctidae)

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3.4.2 Salmonoidei (Osmeridae)

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3.4.3 Stomiatoidei

3.4.3.1 Gonostomatidae - Sternoptychidae

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3.4.3.2 Other Stomatoid Families/Autres familles de poissons stomatoides/ Otras familias de peces estomatoides

- Beebe, W., 1934
Beebe, W. & J. Crane, 1939
Ege, V., 1934; 1948

3.5 Myctophiformes

- Okiyama, M., 1974

3.5.1 Myctophidae

(see Moser and Ahlstrom 1970, for additional references)/(voir Moser et Ahlstrom 1970, pour références supplémentaires)/(véase Moser y Ahlstrom 1970, para otras referencias)

- Moser, H.G. & E.H. Ahlstrom, 1970; 1972; 1974
Pertseva-Ostroumova, T.A., 1964; 1967; 1974
Taning, A.V., 1919

3.5.2 Other Myctophiform Families/Autres familles de poissons myctophiformes/
Otras familias de peces miotefiformes

Anderson, W.W., J.W. Gehringer & F.H. Berry, 1966
Ege, V., 1930; 1953; 1957; 1958
Gibbs, R.H., Jr., 1959
Johnson, R.K., 1971
Merrett, N.R., J. Badcock & P.J. Herring, 1973
Okiyama, M., 1974
Rofen, R.R., 1966; 1966a; 1966b
Zvjagina, O.A., 1965

3.6 Gadiformes

3.6.1 Gadoidei (Gadidae and Related)

Ahlstrom, E.H. & R.C. Counts, 1955
Barans, C.A. & A.C. Barans, 1972
Belyaninam, T.N., 1974
Cipria, G., 1939b
D'Ancona, U. & G. Cavinato, 1965
DeGaetani, D., 1928; 1933
Fischer, W.K., 1959
Gorbunova, N.N., 1954
Marak, R., 1967
Matthews, J.P., & V.v.D. DeJager, 1951
Miller, D. & R.R. Marak, 1959
Mukhacheva, V.A., 1957
Mukhacheva, V.A. & O.A. Zvyagina, 1960
Musick, J.A., 1969; 1974
Santander, H. & O.S. de Castillo, 1969a
Sauskan, V.I. & V.P. Serebriakov, 1968
Schmidt, J., 1905; 1906
Seaton, D.D. & R.S. Bailey, 1971
Yamamoto, G. & C. Nishioka, 1952
Yusa, T., 1954

3.6.2 Ophidioidi

3.6.2.1 Ophidiidae-Brotulidae

Nielsen, J.G., 1966
Sparta, A., 1929; 1932
Wourms, J.P. & O. Bayne, 1973

3.6.2.2. Carapidae

Sparta, A., 1925

3.7 Gobiescoiformes (Gobiesocidae)

Fujita, S. & Y. Dotsu, 1965
Runyan, S., 1961
Shiogaki, M. & Y. Dotsu, 1971; 1971a; 1971b; 1971c

3.8 Lophiiformes

Adams, J.A., 1960
Beretelsen, E., 1951
Fujita, S. & K. Uchida, 1959
Taning, A.V., 1923

3.9 Atheriniformes

3.9.1 Atherinoidei (Atherinidae)

Chirinos de Vildoso, A. & E.D. Chuman, 1964
Ciechowski, J.D. de, 1972
Ehrlich, K.F. & D.A. Farris, 1970; 1971
Foster, N.R., 1968
Hildebrand, S.F., 1922

3.9.2 Exocoetoidei

3.9.2.1 Scomberescoidea

Hatanaka, M., 1956
Hatanaka, M. et al., 1953
Nakamura, S., 1937
Orton, G.L., 1964
Sanzo, L., 1940a
Yusa, T., 1960a

3.9.2.2 Exocoetidae

Gorbunova, N.N. & N.V. Parin, 1963
Hubbs, C.L. & E.M. Kampa, 1946
Kovalevskaya, N.V., 1964; 1965
Kovalevskaya, N.V., N.V. Khrapkova, 1963
Miller, D.J., 1952
Munro, I.S.R., 1954
Parin, N.V. & N.N. Gorbunova, 1964
Tsukahara, H. & T. Shiokawa, 1957
Tsukahara, H., T. Shiokawa & T. Inao, 1957

3.10 Beryciformes

3.10.1 Stephanoberycoidi (Melamphidae)

Ebeling, A.W., 1962
Ebeling, A.W. & W.H. Weed III, 1963; 1973

3.10.2 Holocentridae

McKenney, T.W., 1959

3.11 Lampridiformes

3.11.1 Trachypteroidi

Sanzo, L., 1918; 1925; 1940

3.11.2 Syngnathoidi

Nakamura, S., 1937
Takai, T. & A. Misokami, 1959

3.12 Scorpaeniformes

3.12.1 Scorpaenoidi (Scorpaenidae)

DeLacy, A.C., C.R. Hitt & R.L. Dryfos, 1964
Efremenko, V.N. & L.A. Lisovenko, 1970

Fujita, S., 1957b; 1958; 1959
Fujita, S. & K. Nakurhara, 1955
Hits, C.R., 1962
Mito, S. & K. Uchida, 1958
Morris, R.W., 1956a
Moser, H.G., 1967; 1972; 1974
Orton, G.L., 1955b
Pearcy, W.G., 1962
Phillips, J.B., 1964
Shiokawa, T. & H. Tsukahara, 1961
Takai, T. & T. Fukunaga, 1971
Taning, A.V. 1961
Tsukahara, H., 1962
Waldron, K.D., 1968
Wales, J.W., 1952

3.12.2 Cottoidei

3.12.2.1 Cottidae

Bolin, R.L., 1941
Cowan, G.I. McT., 1970
Fujita, S., 1957
Gorbunova, N.N., 1964
Khan, N.Y. & D.J. Faber, 1974
Kyushin, K., 1970
Morris, R.W., 1951
O'Connell, C.P., 1953
Stein, R., 1973
Tsukahara, H., 1952
Zvjagina, O.A., 1963

3.12.2.2 Cyclopteridae

Kobayashi, K., 1962b

3.12.3 Hexagrammoidei

3.12.3.1 Hexagrammidae

Abe, T., 1951
Gorbunova, N.N., 1962
Kobayashi, K., 1958
Orlov, Yu I. & L.V. Polikashin, 1962
Yusa, T., 1967

3.12.3.2 Anoplopomatidae

Brock, V.E., 1940
Kobayashi, K., 1957
Kodolov, L.S., 1968

3.12.4 Platycephaloidei (Platycephalidae)

Fujita, S. & M. Uneno, 1956

3.13 Perciformes

3.13.1 Percoidei

Norcross, J.J. et al., 1974

3.13.1.1. Bramidae

Mead, G.W., 1972
Okada, Y. & K. Suzuki, 1956
Sanzo, L., 1928
Schmidt, J., 1918a

3.13.1.2. Branchiostegidae

Fisher, W.K., 1958
Okiyama, M., 1964

3.13.1.3. Carangidae

Ahlstrom, E.H. & O.P. Ball, 1954
Aprieto, V.L., 1974
Berry, F.H., 1959
Ciechowski, J.D. de & G. Weiss, 1973
Comand, F. & C. Franqueville, 1973
Demir, M., 1971
Demir, N., 1958
Fields, H.M., 1962
Haigh, E.H., 1972a
Kakamura, S., 1936
McKenney, T.W., E.C. Alexander & G.L. Voss, 1958
Miller, J. & B.Y. Sumida, 1974
Mitani, F., 1960
Nakamura, S., 1936a
Okiyama, M., 1970
Santander, H. & O.S. de Castillo, 1971
Sanzo, L., 1931; 1933
Sohankenbeck, W., 1931
Uchida, K. et al., 1958

3.13.1.4 Centropomidae

Chua, T.E., 1970

3.13.1.5 Chaetodontidae

Fujita, S. & S. Mito, 1960

3.13.1.6 Coryphaenidae

Mito, S., 1960

3.13.1.7 Kyphosidae

Kobayashi, K. & M. Igarashi, 1961
Mito, S., 1957a

3.13.1.8 Leiognathidae

Fujita, S., 1970

3.13.1.9 Oplegnathidae

Mito, S., 1956a

3.13.1.10 Pomacentridae

Fujita, S., 1957a
Limbaugh, C., 1964
Shaw, E.S., 1955
Turner, C.H. & E.E. Ebert, 1962

3.13.1.11 Priacanthidae

Caldwell, D.K., 1962

3.13.1.12 Rachycentridae

Dawson, C.E., 1971

3.13.1.13 Sciaenidae

Fujita, S., 1956b
Meyer-Rochow, V.B., 1972
Pearson, J.C., 1941
Welsh, W.W. & C.M. Breder, Jr., 1923

3.13.1.14 Serranidae

Guitart, M.D. & M.J. Fernandes, 1966
Kendall, A.W., Jr., 1972
Mito, S., 1957
Presley, R., 1970
Ukaiwa, M., M. Higuchi & S. Mito, 1966

3.13.1.15 Sillaginidae

Ueno, M. & S. Fujito, 1954

3.13.1.16 Sparidae

Cassie, R.M., 1956
Ciechomski, J.D. de & G. Weiss, 1973b
Mito, S., 1956
Sikama, Y., 1961

3.13.2 Acanthuroidei

Cipria, G., 1940
Fujita, S. & M. Ueno, 1954
Randall, J.E., 1961

3.13.3 Ammodytoidei

Einarsson, H., 1951; 1955
Kobayashi, K., 1961b
Macer, C.T., 1967
Norcross, J.J., W.H. Massmann & E.B. Joseph, 1961
Williams, G.C., S.W. Richards & E.G. Farnworth, 1964

3.13.4 Blennioidei

3.13.4.1 Blennidae

Cipria, G., 1934; 1936
Fives, J., 1970
Ford, E., 1922
Mito, S., 1954
Munro, I.S.R., 1955
Raju, S.N., 1971

3.13.4.2 Anarhichadidae

Kobayashi, K., 1961

3.13.4.3 Clinidae

Sparta, A., 1948a

3.13.4.4 Stichaeidae

Fujita, S. & K. Uchida, 1959a
Schultz, L.P. & A.C. Delacy, 1932

3.13.4.5 Ptilichthyidae

Kobayashi, K., 1961a

3.13.5 Gobioidae

Dotu, Y., 1954; 1955; 1955a; 1955b; 1956; 1956a; 1957; 1957a; 1957b; 1957c
1957d; 1958; 1958a; 1958b; 1958c; 1959; 1959a; 1961
Dotu, Y. & S. Mito, 1955; 1955a; 1958
Dotu, Y., S. Mito & M. Ueno, 1955
Dotu, Y. & M. Shioyaki, 1971
Dotu, Y. & T. Tsutsumi, 1959
Ebert, E.E. & C.H. Turner, 1962
Lebour, M.V., 1919
Nakamura, S., 1936
Shmove, Yu. V., 1971
Sparta, A., 1934; 1934a; 1936; 1950
Weisel, G.F., Jr., 1947

3.13.6 Icesteidae (Icesteidae)

Allen, G.H., 1968

3.13.7 Labroidae

3.13.7.1 Labridae

Bolin, R.L. 1930
Cipria, G., 1939
Kubo, I., 1939
Salekhova, L.I., 1971
Sparta, A., 1930; 1931; 1932a; 1933; 1936a; 1936b; 1948

3.13.7.2 Family Scaridae

Cipria, G., 1939a
Winna, H.E. & J.E. Bardach, 1960

3.13.8 Mugiloidei (Mugilidae)

- Altan, H., 1957a
Anderson, W.W., 1957; 1958
Pillay, S.R., 1972
Sanzo, L., 1936
Tung, I.S., 1973
Ysahouv, A. & E. Berner-Samsonov, 1970

3.13.9 Scombroidei

- Gorbunova, N.N., 1974
Jones, S. & M. Kumaran, 1964

3.13.9.1 Scombridae

(For additional references refer to Richards and Klawe, 1972)/(voir Richards et Klawe, 1972 pour références bibliographiques supplémentaires)/(véase Richards y Klawe, 1972 para otras referencias bibliográficas)

- Boonprakob, U. & Y. Dhebtaranan, 1972
Ciechomski, J.D. de, 1971c
Dekhnik, T.V., 1959
Fry, D.H., Jr., 1936
Gorbunova, N.N., 1974
Harada, T., O. Murata & H. Furutani, 1973
Harada, T., O. Murata & S. Migashito, 1973
Klawe, W.L., 1961; 1966
Kramer, D., 1960
Matsui, T., 1970
Matsumoto, W.M., 1958; 1959; 1967
Matsumoto, W.M. et al., 1972
Mori, K., 1967
Mori, K., S. Ueyanagi & Y. Nichikawa, 1971
Potthoff, T., 1974
Richards, W.J. & G.R. Dove, 1971
Richards, W.J. & W.L. Klawe, 1972
Richards, W.J. & T. Potthoff, 1974
Roedel, P.M., 1949
Sanzo, L., 1932
Scaccini, A. et al., 1973
Ueyanagi, S., 1969
Wade, C.B., 1951
Watanabe, H. et al., 1966
Watanabe, T., 1970
Wollam, M.B., 1969; 1970
Yasutake, H., G. Nishi & K. Mori, 1973
Yoshida, H.O., 1971

3.13.9.2 Gempylidae and Trichiuridae

- DeJager, D.v.D., 1955
Jones, S., 1960
Strasburg, D.W., 1964
Struberg, A., 1918
Tsukahara, H., 1961
Voss, N.A., 1954
Wiktor, K., 1970

3.13.9.3 Istiophoridae - Xiphiidae

- Arata, G.F., Jr., 1954
Bartlett, M.R. & R.L. Haedrich, 1968
Caldwell, D.K., 1962
DeSylva, D.P., 1963
Eschmeyer, W.N. & H.R. Bullis, Jr., 1968
Gehring, J.W., 1956; 1970
Gorbunova, N.N., 1969
Jones, S. & M. Kumaran, 1964
Laurs, R.M. & R.N. Nichimoto, 1970
Nakamura, I., 1968
Sanzo, L., 1922; 1930
Sella, M. 1911
Sparta, A., 1953; 1961
Taning, A.V., 1955
Tibbo, S.N. & L.M. Lauzier, 1969
Ueyanagi, S., 1959; 1960; 1960a; 1962; 1962a 1963; 1964; 1964a; 1974; 1974a
Ueyanagi, S. & H. Yabe, 1959
Ueyanagi, S. et al., 1970
Voss, G.L., 1953
Yabe, H., 1951
Yabe, H. et al., 1959

3.13.10 Sphryaenoidei (Sphryaenidae)

- Houde, E.D., 1972
Orton, G.L. 1955a
Shojima, Y., S. Fujita & K. Uchida, 1957

3.13.11 Stromateoidei

- Colton, J.B. & K.A. Honey, 1963
Grey, M., 1955
Legaspi, V.A., 1956
McKenney, T.W., 1961
Mito, S. & T. Senta, 1967
Sanzo, L., 1932a
Sparta, A., 1929a; 1946

3.13.12 Trachinoidei

- Mito, S., 1956b; 1962

3.14 Pleuronectiformes

3.14.1 Bothidae

- Amaoka, K., 1964; 1970; 1971; 1972
Dekhnik, T.V., 1971
Deubler, E.E., 1958
Futch, C.R., 1971
Futch, C.R. & F.H. Hoff, Jr., 1971
Gutherz, E.J., 1971
Leonard, S.B., 1971
Miller, D. & R. Marak, 1962
Nielsen, J.G., 1963
Ochiai, A. & K. Amaoka, 1963
Okiyama, M., 1967
Richardson, S.L. & E.B. Joseph, 1973
Smith, W.G. & M.P. Fahay, 1970
Uchida, K., 1936

3.14.2 Pleuronectidae

Adron, J.W. et al., 1974
Dekhnik, T.V., 1959a
Fujita, S., 1965
Hagerman, F.B., 1952
Harry, G.Y., 1959
Hickman, C.P., Jr., 1959
Jensen, A.S., 1935
Musienko, L.M., 1954
Nichols, J.H., 1971
Okiyama, M., 1963
Orcutt, H.G., 1950
Orsi, J.J., 1968
Orton, G.L. & C. Limbaugh, 1953
Pearcy, W.G., 1962
Pertseva-Ostroumova, T.A., 1953; 1954; 1960; 1961
Petersen, C.G.J., 1904
Porter, P., 1964
Rapson, A.M., 1940
Robertson, D.A. & U. Raj, 1971
Schmidt, J., 1904
Takita, T. & S. Fujita, 1964
Takita, T., S. Fujita & Y. Sotsu, 1967
Taning, A.V., 1936
Van Cleve, R., 1936
Yusa, T., 1957; 1957a; 1958; 1960; 1960b; 1961; 1974

3.14.3 Scophthalmidae, Soleidae, Cynoglossidae

Balal Krishnan, K.P. & C.B.L. Devi, 1974
Bensam, P., 1969
Fujita, S. & T. Takita, 1965
Fujita, S. & K. Uchida, 1957
Futch, C.R., 1970
Houde, E.D., C.R. Futch & R. Detwyler, 1970
Jones, A., 1972
Moore, E., 1947

3.14.4 General/Général/General

Papers dealing with life histories of fishes belonging to two or more families of flatfishes/Documents concernant le cycle de vie des poissons appartenant a deux ou plusieurs familles de soles/Documents referentes al ciclo vital de peces pertenecientes a dos o más familias de lenguados

Balakrishnan, K.P. & C.B.L. Devi, 1974
Hsiao-wei, C., X. Gui-Pen & X. Shashen, 1965
Kyle, H.W., 1913
Pertseva-Ostroumova, T.A., 1965

3.15 Tetraodontiformes

Zharov, V.L. & A.M. Zhudova, 1967
Zhudova, A.M., 1969

3.15.1 Tetraodontidae

Fujita, S., 1956; 1956a; 1966
Fujita, S. & M. Ueno, 1956a
Shojima, Y., 1957

3.15.2 Triacanthidae

Ohsima, Y. & N. Nakamura, 1941

3.15.3 Molidae

Sherman, K., 1961

4. REFERENCES ON SPECIES IDENTIFICATION OF EGGS AND LARVAE, GROUPED GEOGRAPHICALLY/REFERENCES SUR L'IDENTIFICATION DES ESPECES D'OEUFs ET DE LARVES, GROUPEES SELON DES CRITERES GEOGRAPHIQUES/BIBLIOGRAFIA SOBRE IDENTIFICACION DE ESPECIES DE HUEVOS Y LARVAS, POR REGIONES GEOGRAFICAS

4.1 Northwest Atlantic/Atlantique nord-ouest/Atlántico noroeste

Bigelow, H.B. & W.C. Schroeder, 1953

Dannevig, A., 1919

Kuntz, A. & L. Radcliffe, 1917

Mansueti, A.G. & J.D. Hardy, Jr., 1967

Mansueti, R. (comp.), 1954

Shih, G.T., A.J.G. Figueira & E.H. Grainger, 1971

4.2 Northeast Atlantic/Atlantique nord-est/Atlántico nordeste

Arbault, S. & N. Boutin, 1968

Ehrenbaum, E., 1905 & 1909

Einarsson, H., 1966

Hureau, J.C. & Th. Monod, 1973

Kazanova, I.I., 1953

Kiliachen Kova, V.A., 1970

Rass, T.S., 1949

4.3 Mediterranean and Black Sea/Mediterrané et Mer noire/Mediterráneo y Mar Negro

Aboussouan, A., 1964

Arim, N., 1957

D'Ancona, U. et al., 1931 to 1956

Demir, N., 1969

Fage, L., 1918

Hureau, J.C. & Th. Monod, 1973

Marinero, J.Y., 1971

Vodjaniskii, V.A. & I.I. Kazanova, 1954

4.4 Northwest Pacific/Pacifique nord-ouest/Pacífico noroeste

Day, D.S. et al., 1971

Mito, S., 1960a; 1960b; 1961; 1961a; 1961b; 1962; 1962a; 1962b; 1962c; 1963; 1963a; 1963b; 1963c

Shih et al., 1971

Uchida, K. et al., 1958

4.5 Northeast Pacific/Pacifique nord-est/Pacífico nordeste

No comprehensive paper/Aucune étude compréhensive/Ninguna referencia comprensiva

4.6 Eastern Central Atlantic/Atlantique centre-est/Atlántico centro-oriental

Aboussouan, A., 1965; 1966; 1966a; 1967; 1968; 1968a; 1968b; 1972; 1972a; 1972b
Zhudova, A.M., 1969

4.7 Western Central Atlantic/Atlantique centre-ouest/Atlántico centro occidental

Hildebrand, S.F. & L.E. Cable, 1931; 1938

Rass, T.S., 1972

Silva, D.P. de & L.N. Scotton, 1972

4.8 Indian Ocean Coastal Waters/Eaux côtières de l'océan Indien/Aguas costeras del océano Índico

Jones, S., 1951

Jones S. & P. Bensam, 1968

Rass, T.S., 1968

4.9 Western Central Pacific/Pacifique centre-ouest/Pacífico centro-occidental

Delsman, H., 1921; 1922; 1924; 1925; 1926; 1926a; 1926b; 1929; 1930; 1930a; 1930b; 1931; 1931a; 1932; 1933; 1938

Tseng, W.Y. et al., 1971

Vatanachai, S., 1972

4.10 Eastern Central Pacific/Pacifique centre-est/Pacífico centro-oriental

Ahlstrom, E.H., 1965a

Barnhart, P.S., 1927; 1932

Budd, P.L., 1940

David, L.R., 1939

Orton, G.L., 1953

4.11 Southwest Pacific/Pacifique sud-ouest/Pacífico sudoeste

Graham, D.H., 1939

Jillett, J.B., 1968

Munro, I.S.R., 1945

Thomson, G.M. & T. Anderson, 1929

4.12 Southeast Pacific/Pacifique sud-est/Pacífico sudeste

No comprehensive references/Aucune étude compréhensive/Ninguna referencia comprensiva

4.13 Southwest Atlantic/Atlantique sud-ouest/Atlántico sudoeste

Aboussouan, A., 1969

Ciechomski, J.D. de, 1968; 1971a

4.14 Southeast Atlantic/Atlantique sud-est/Atlántico sudeste

Gilchrist, J.D.F., 1916

Haigh, E.H., 1972

Meyer-Rochow, V.B., 1972

Richards, W.J., 1969

4.15 Oceanic Resources/Ressources océaniques/Recursos oceánicos

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Scombridae: see/voir/ver Richards, J.W. and W.L. Klawe (1972).

5. REPORTS OF SURVEY RESULTS GROUPED GEOGRAPHICALLY/RAPPORTS SUR LES RESULTATS DES PROSPECTIONS, GROUPEES SELON DES CRITERES GEOGRAPHIQUES/INFORMES SOBRE RESULTADOS DE RECONOCIMIENTOS, POR REGIONES GEOGRAFICAS

5.1 Northwest Atlantic/Atlantique nord-ouest/Atlántico noroeste

Bainbridge, V. & G.A. Cooper, 1971
Boyar, H.C. et al., 1971
Chenoweth, S.B., 1973
Clark, J.R. et al., 1969; 1970
Day, L.R., 1961
Dovel, W.A., 1971
Fahay, M.P., 1974
Graham, J.J., 1972; 1972a
Graham, J.J. & N.B. Boyar, 1965
Graham, J.J., S.B. Chenoweth & C.W. Davis, 1972
Graham, J.J. & C.W. Davis, 1971
Graham, J.J. & P.M.W. Venno, 1968
Hansen, P., 1968; 1968a
Henderson, G.T.B., 1968
Herman, S.S., 1963
L'Harrow, R. & D. Briand, 1972
Magnusson, J., 1968; 1968a
Marak, R., 1974
Marak, R. & J.B. Colton, Jr., 1961
Marak, R., J.B. Colton, Jr. & D.B. Foster, 1962
Marak, R., et al., 1962
Messeih, S.W., S.N. Tibbo & L.M. Leusier, 1971
Richards, S.W., 1959; 1973
Sameoto, D.D., 1972
Scott, J.S., 1972
Serebrayakov, V.P., 1965
Smidt, E., 1968
Smith, W.G., 1973
Tibbo, S.N. et al., 1958
Wells, R., 1968
Wheatsland, S.B., 1956
Wilkins, E.P.H. & R.M. Lewis, 1971

5.2 Northeast Atlantic/Atlantique nord-est/Atlántico nordeste

Arbault, S. & N. Lacroix, 1969; 1970
Arbault, S. & N. Boutin, 1971
Bainbridge, V., G.A. Cooper & P.J.B. Hart, 1974
Bannister, R.C.A., D. Harding & S.J. Lockwood, 1974
Baranenkova, A.S. & N.S. Khoklina, 1961; 1968; 1968a
Cushing, D.H., 1957
Dickson, R.R., J.G. Pope & M.J. Holden, 1974
Dragesund, O., 1970
Fives, J.M., 1970
Grauman, G.B., 1972
Hansen, V. Kr. & K.P. Andersen, 1961
Hart, P.J.B., 1974
Henderson, G.T.D., 1961; 1961a; 1968
Hyronimus, E., 1971
Jones, R. & W.B. Hall, 1974
Lindquist, A., 1972; 1972a
Mankowski, W., 1948
Nellen, W. & G. Hempel, 1970

Postuma, K.H. & J.J. Zijlstra, 1974
 Riley, J.D., 1974
 Russel, F.S., 1969; 1973
 Russel, F.S., & N. Demir, 1971
 Saville, A., 1971
 Saville, A., I.G. Paxter & D.W. McKay, 1974
 Seliverstov, A.S., 1974
 Southward, A.J. & N. Demir, 1974
 Wiborg, K.F., 1960
 Williams, R. & P.J.B. Hart, 1974
 Wyatt, T., 1974

5.3 Mediterranean and Black Sea/Méditerranée et Mer noire/Mediterráneo y Mar Negro

Aldebert, Y. & H. Fournier, 1971
 Brezeanu, G., 1961
 Dekhnik, T.V., 1954; 1968
 Dekhnik, T.V. & V.I. Sinyoukova, 1964; 1966
 Einarsson, H. & N. Gurturk, 1960
 Furneston, M.L., 1971
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 Hart, J.L., 1943
 Ketchen, K.S., 1956
 Lebrasseur, R.J., 1964; 1970
 Lebrasseur, R.J. et al., 1969
 Levings, C.D., 1968
 McHugh, J.L., 1942; 1942a
 Robinson, D.G., 1969
 Robinson, D.G., W.E. Barraclough & J.D. Fulton, 1968; 1968a
 Smith, R.T., 1940
 Stevenson, J.C., 1947; 1949; 1962
 Thompson, W.F. & R. Van Cleve, 1936
 Van Cleve, R. & A.H. Seymour, 1953
 Waldron, K.D., 1970; 1972

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Aboussouan, A., 1971
 Castle, P.H.J., 1966
 Conand, F., 1970; 1973
 Conand, F. & J.L. Cremoux, 1972
 Dessier, A. & R. Pianet, 1971
 Fagetti, E., 1970
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 Krzelj, S., 1972; 1972a
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 Wiktor, K., 1969

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Arnold, E.L., Jr. & J.R. Thompson, 1958
 Caldwell, M.C., 1962
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 Dekhnik, T.V., M. Juarez & M. Salabaria, 1966
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 Dwinell, S.E. & C.R. Futch, 1973
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 Houde, E.D., 1973
 Jannke, T.E., 1971
 Lopez, R.H., 1972
 Rass, T.S. & M. Juarez, 1967
 Smith, D.G., 1968
 Wilkens, E.P.H., 1974

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Ahlstrom, E.H., 1966
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 Peter, K.J., 1967; 1970; 1974

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 Gorbunova, N.N., 1971
 Tseng, W.Y. & C.H. Liu, 1971; 1972
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5.10 Eastern Central Pacific/Pacifique centre-est/Pacifico centro-oriental

Ahlstrom, E.H., 1943; 1948; 1952; 1954; 1956; 1958; 1959; 1959a; 1959b; 1960; 1961; 1965
 1966a; 1967; 1968; 1968a; 1969; 1969a; 1971; 1972; 1972a
 Ahlstrom, E.H. & H.D. Casey, 1956
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 Clemens, H.B., 1956
 Farris, D.A., 1958; 1962; 1963
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 Isaacs, J.D., 1964; 1965
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 Kramer, D. 1963; 1970
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 Kramer, D. & P.E. Smith, 1970; 1970a; 1970b; 1970c; 1971; 1971a; 1971b; 1972; 1973
 Lasker, R., 1970
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 Richards, S.L., 1973
 Sette, O.E. & E.H. Ahlstrom, 1948
 Silliman, R.P., 1943; 1943a; 1946
 Smith, P.E., 1972; 1973
 Smith, P.E., E.H. Ahlstrom & H.D. Casey, 1970

5.11 Southwest Pacific/Pacifique sud-ouest/Pacifico sudoeste

Castle, P.H.J., 1964
 Veyanagi, S., 1969a

5.12 Southeast Pacific/Pacifique sud-est/Pacifico sudeste

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 Brandhorst, W. & O. Rojas, 1967; 1968
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Ochoa, N., 1966
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5.13 Southwest Atlantic/Atlantique sud-ouest/Atlántico sudeste

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Ciechomski, J.D. de & E. Boschi, 1968
Ciechomski, J.D. de & D.A. Capezzani, 1973
Ciechomski, J.D. de & G. Weiss, 1973a; 1973b; 1974; 1974a
Matsuura, Y., 1971; 1971a
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Davies, D.H., 1956; 1957
DeJager, B.v.D., 1954
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Changes in Saltwater Angling Methods and Gear in California

SUSAN E. SMITH

Introduction

In California, as in most other coastal states, saltwater recreational fishing has increased rapidly over the years, and is likely to continue to increase. Recreational fish stocks, however, only have the capacity to yield a limited sustained catch.

To manage a recreational fish stock rationally, its relative abundance must be monitored over a period of time. One method widely used in assessing relative abundance is the collection and analysis of catch per unit of effort data (i.e., catch per angler hour, catch per angler day). Researchers recognize, however, that there are other factors to consider when assessing abundance by this technique. One such factor is the change in efficiency of fishing gear and methods over a period of time. Actual reduction of fish stocks, if measured by catch-per-effort alone, may be masked by increased efficiency in gear and/or methods, so that there would appear to be little, if any, decline in the stock (Gulland, 1968).

One of the first steps in approaching and understanding this problem is to document important changes in angling techniques and tackle, and the approximate times these changes have taken place. Descriptions of commercial fishing gear and methods have been documented by Scofield (1929, 1947, 1948, 1951a, 1951b, 1956), Fry

(1931), Whitehead (1931), Croker (1938a), and others. Information on commercial gear and techniques has also been gathered by the State of California since 1916. This type of information is not available for California's marine recreational fisheries, except in scattered reports in the scientific literature and in popular articles.

This report traces developments in saltwater angling equipment from just before the turn of the century to the present. It also presents some examples of California fisheries that have been affected by developments in sportfishing methods and equipment, and documents current methods and tackle used in these fisheries.

General Developments

California saltwater recreational fishing had its beginnings during the last decades of the 19th century. In the early days of the sport, it appears that most offshore fishing was conducted with handlines, except for a select group of big game anglers who fished for bluefin tuna off Catalina Island and a few salmon trollers in Monterey Bay (Collins, 1892; Holder, 1914; French, 1916). No doubt some people used fly-fishing and freshwater baitcasting tackle for some of the smaller inshore and anadromous species around river mouths and in creeks and bays, but there is little specific information of the type of tackle used in these areas.

Hexagonal split bamboo rods had been introduced in the United States around 1870 (Marden, 1965), and rods made of plain bamboo (Calcutta type) were also available before the turn of

the century, as were a variety of hardwood rods made of Cuban lancewood, hickory, South American greenheart, and bethabera. Multiplying baitcasting reels¹ were in use, but only a few were designed for saltwater fishing. Because these early multipliers did not have an internal drag or free-spool mechanism, the reel handles would spin wildly when casting or when a fish ran with the line. For this reason they were coined "knucklebusters." Pressure was applied to the outgoing line by a leather thumb brake.

Fishing line was usually tarred cotton or twisted linen. The last, called "cuttyhunk," became the most popular for saltwater use and consisted of strands of Irish linen. Each strand or ply of the most common type (25-lea²) had a breaking strength of about 3 pounds per strand dry, and 5 pounds wet; a more specialized line (50-lea) tested at 2 pounds per strand when dry and 3 pounds when wet (A. W. Agnew, Sunset Line and Twine, Petaluma, Calif., pers. commun.). Cuttyhunk became the standard in ocean angling until supplanted by nylon and Dacron³ after the second World War. Linen line was combined with a variety of leader materials, usually gut or wire.

¹Multiplying reels, as opposed to single-action types, are geared to give increased retrieving speed, the spool revolving several times with each turn of the handle.

²A unit of measurement (300 yards per pound) indicating the degree of fineness of the yarn from which the threads of the line were made.

³Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

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During the mid-1890's, gasoline boat engines were developed (Scofield, 1956), which would have a profound effect on the expansion of ocean sport fishing on the west coast. After the turn of the century a steadily increasing number of boats began to shift from sail and oar power to gasoline engine power.

One of the most important developments in ocean fishing tackle was the invention of the star-drag reel. The first reel (Fig. 1) of this type with slipping clutch (internal drag) and irreversible handle was patented by Edward Vom Hofe and Co. in 1902 for big game fishing off Catalina (Major, 1948; Melner and Kessler, 1972). After about 1913, the Vom Hofe star drag and other similar reels began to replace the early knucklebusters (Major, 1948; Reiger, 1973), but apparently they were mostly used by big game fish anglers and still quite expensive. In a 1919 catalogue, prices for the Universal Star (Vom Hofe) in sizes 2/0 to 9/0 ranged from \$57.50 to \$75.50 each (Melner and Kessler, 1972).

The 1920's marked a turning point in ocean fishing with the introduction of public sportfishing boats and fishing barges in southern California (Major, 1948; Van Deventer, 1926; Sadler, 1928). In general, a sportfishing boat or party boat⁴ provides fishing space to the public for a fee and operates on a scheduled basis as opposed to charters and rentals where the boat itself is hired for the exclusive use of one or more anglers. Barges are essentially immobile sportfishing boats reached by shuttle launches from shore. With these new facilities, open ocean fishing became available to the general public.

In the 1930's, live-bait fishing and public sportfishing (Fig. 2) became established in southern California, while ocean pleasure fishing was just beginning or already underway in

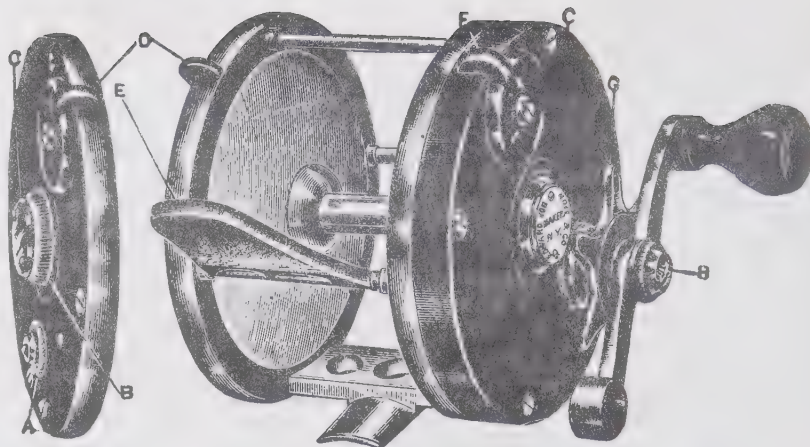


Figure 1.—Vom Hofe & Company's "Universal Star," forerunner of today's star-drag reel design, as it appeared in a 1919 catalog (E=removable leather thumb pad, F=free-spool lever, G=star drag). Taken from *Great Fishing Tackle Catalogs* edited by Samuel Melner and Hermann Kessler. Commentary by Sparse Grey Hackle. ©1972 by Samuel Melner and Hermann Kessler. Introduction and commentary ©1972 by Alfred W. Miller. Used by permission of Crown Publishers, Inc.



Figure 2.—Pierfishing for mackerel at Monterey, Calif., in 1931. Note long bamboo poles (no reels) and thick lines. Mass-produced, low-cost star-drag reels came on the market about 4 years after this photo was taken. (Photo courtesy of California Department of Fish and Game.)

⁴In this report the term "sport fishing boat" has been substituted for, and is synonymous with, "partyboat." Use of the latter term has been discouraged by members of the recreational fishing industry.

northern California (Croker, 1938b; Davis, 1949). Starting in 1935, California boat operators who carried anglers for hire were required by law to keep daily records of their catch.

During the mid-1930's, American reel manufacturers introduced moderately priced, mass-produced, high quality, revolving spool reels (star-drag type) to middle and low income people, and these reels soon came into widespread use (H. Henze, Penn Reels, Philadelphia, Pa., pers. comun.). Although the first spinning (fixed spool) reel was introduced from France in 1935, by the time a market was developed in 1939, the supply was cut off because of the war (McClane, 1974). Braided nylon fishing line made its appearance around 1939 (samples were exhibited at the San Francisco World's Fair), and it later came into limited use during the war years (A. W. Agnew, Sunset Line and Twine, Petaluma, Calif., pers. commun.). This early nylon line stretched badly, and at the time, no one knew how to eliminate or reduce the stretch factor. In general, bamboo was the most popular rod material, although in 1936, tubular metal rods made of beryllium copper came on the market. These beryllium rods resisted saltwater corrosion better than other metal rods already on the market for freshwater use (Moss, 1976), although corrosion was still a problem.

When the United States entered World War II in December 1941, the U.S. Navy closed all ports to sport-fishing. Later a few boats with special permits were allowed to operate from certain ports, but under strict regulations (Young, 1969).

By the end of the war, most anglers were still using cane rods, star-drag reels, and twisted linen line with gut or wire leaders, but important developments in tackle were already underway. Many reels were now equipped with lightweight plastic spools which made it much easier to cast light lures and live bait using cuttyhunk line. Also, by this time, the gear-in-mesh feature was available on most reels. Prior to this invention it was very easy to strip the gears of a reel if the angler threw it into gear while a fish was running with the line.

An important new product, monofilament nylon line, was introduced in 1946. Although the first monofilament line was waterproof (did not rot) and was lighter than braided nylon or linen line, it was stiff and difficult to use as a main line. It also stretched badly and played havoc with plastic spool reels, bursting them under pressure. Later, many improvements were made that cut down on the stretch, and casting lines were made softer and limper. Soft monofilament was finally introduced to the west coast in the early 1950's, but it did not begin to outsell braided linen line until the early 1960's when spin fishing became popular in salt water. Spinning reels had been reintroduced about the same time as monofilament line (circa 1946), but these were mainly designed for freshwater fishing. The early spinning reels were trouble-prone and did not work well with braided line which was still popular for ocean fishing in the 1940's.

An important advance in rod building occurred in 1948, when fiberglass rods were introduced, and solid, hollow, and wooden core models became available (Major, 1948). The advantage of fiberglass was that it was flexible and tough, excellent for casting, and did not take a permanent bend or "set" after prolonged use as did bamboo or hardwood rods, or rust like metal rods.

Also, in the late 1940's, the first fiberglass boats were made available to the public. Fiberglass enabled boat builders to mass produce one-piece hulls with a minimum of skilled labor, and in following years this material would become a standard in the pleasure boat field (Whittier, 1976). Advancements in welded and riveted aluminum hulls also helped to make aluminum a popular boat-building material. These new materials made fishing skiffs strong yet light and portable, and relatively maintenance free.

Another postwar development was the introduction of outboard engines with forward-neutral-reverse gearshifts. These soon replaced the old direct drive outboards, making small boats more manageable, safer, and simpler to operate. Soon afterward manufacturers offered cable-operated remote-control steering so one could operate

the motor from up forward, giving the boat better stability and the skipper better forward visibility (Whittier, 1976). These developments, as well as the many other improvements in boat and engine designs that followed after the war, including the introduction of electric starters, radio-telephones, fathometers, radar, and other electronic equipment, had a great influence on the expansion of the recreational boat fishery in California.

In 1950, soft monofilament fishing line was introduced on the west coast. Soon most leader materials were discarded in favor of tying the hook directly to the monofilament line. This made casting small baits and lures easier and caused a boom in the lure business (Agnew, Sunset Line and Twine Co., Petaluma, Calif., pers. commun.; Cannon, 1964). Also, during this time, fiberglass rods were quickly replacing the old cane rods. Moderately priced, quality spinning reels were introduced in 1953, and these reels soon became popular in freshwater fishing, and later (the 1960's) in saltwater fishing. The spinning reel, or fixed-spool design, eliminated the main cause of line backlashes, permitted the use of very light lures and baits, and perhaps most important, made the art of casting relatively easy to master for novice anglers.

In the late 1950's, the Coast Guard enforced stringent regulations for passenger boats (Frey, 1971), and the following years would see a marked decrease, followed by a leveling off, in the number of active sportfishing boats (Young, 1969), and a trend, especially in southern California, toward larger, faster, and more comfortable boats designed for offshore and long-range fishing trips. Many of the larger southern California sport boats were built and launched during this period (Young, 1969).

In the 1960's, the combination of spinning reels, fiberglass rods, and monofilament nylon line became established in saltwater fishing in California. On the west coast, monofilament line came into widespread use, outselling braided line (Agnew, Sunset Line and Twine, Petaluma, Calif., pers. commun.). By the mid-1960's, fiberglass had dominated the rod market.

Today, nylon monofilament line is still the most popular line, and is used on both spinning and revolving spool reels. Spinning gear is especially popular for the many small-to-medium-sized game fishes found in California's inshore waters. Revolving spool reels are enjoying renewed popularity largely due to refinements in reel designs. Some of the newer reels have an internal centrifugal brake system as well as an external spool tension control that allows the angler to cast lures and baits with monofilament line without line backlashes—the main drawback of old revolving-spool reels. Spinning tackle is now common on southern California live-bait sportfishing boats, although the combination of conventional (revolving-spool) reels and monofilament line is widely used, and is also preferred for ocean salmon trolling and sturgeon fishing in northern California, and jigging for some of the larger game fish in southern California.

Braided lines (nylon and Dacron) are generally reserved for big-game trolling and offshore bottom fishing where heavy duty conventional reels and rods are used. A new type of small diameter braided Dacron line has recently been introduced and is gaining in popularity in southern California. It has good abrasion resistance and low stretch (7-8 percent as compared with nylon line with 20-25 percent stretch).

The tubular fiberglass rod is still the standard in California sport fishing; however, a new type of rod made from graphite was introduced around 1973. Graphite rods are extremely light and ultrasensitive, yet very strong, though approximately one-third smaller in diameter than comparable fiberglass rods. At this time, however, graphite rods are still quite expensive.

Finally, the downrigger (Fig. 3), used for deep-water trolling, is showing up on an increasing number of private sportfishing boats in California. This device allows the angler to fish at a bait at accurately controlled depths with light or medium tackle and land a fish without the hindrance or loss of the sinker. The downrigger is clamped to the side or stern of the boat and consists of a short rod and hand-

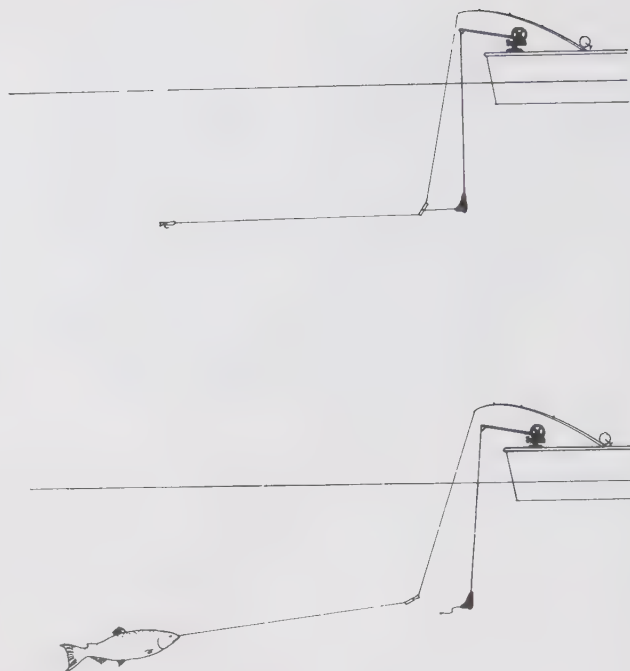


Figure 3.—The downrigger allows an angler to fish a bait or lure at accurately controlled depths using light tackle. When a fish strikes, the angler's line is released from the downrigger sinker and line.

cranked or electrically operated metal drum loaded with stainless steel wire weighted at the end with a heavy cannonball or diving sinker. The angler's unweighted line is attached to the weighted downrigger line by a metal sinker release or release clip, then lowered to the desired depth. When a fish strikes the bait, the angler's line is released, allowing him to fight and land his fish on the free line.

Fishing Technique and Tackle Changes

The following are just a few examples of specific marine recreational fisheries in California that have been affected by developments in sportfishing tackle and fishing methods. No doubt other fisheries have been affected as well. These examples are also used to document present methods and tackle.

San Francisco Area Striped Bass Fishery

Up until the mid-1950's, striped bass, *Morone saxatilis*, fishing methods in San Francisco Bay had remained essentially the same for about half a century—still-fishing with bait and near-surface trolling with artificial lures. But in the summer of 1957, a collapse of the ocean salmon fishery brought salmon sport fishing boats into the bay to fish for striped bass in deep water using the new technique of deep-line trolling with 3-pound (1.4-kg) sinkers and sinker releases (Chadwick, 1962). Many bass were caught, that year off Alcatraz Island, and subsequently in other areas in upper San Francisco Bay. From 1957 to 1959, most fish caught in the upper bay were taken by deep-line trolling. Furthermore, a winter fishery developed around 1958 when anglers discovered

that striped bass could be taken during the herring spawning runs. They used both the new deep-line trolling technique and the standard surface trolling method. Chadwick (1962) concluded that because fishing techniques in upper San Francisco Bay had changed so radically (Fig. 4), the commercial sport fishing boat catch could not be used to measure changes in abundance of striped bass.

From the early to mid-1960's, another major change occurred in striped bass methods with the introduction of live bait drifting with anchovies, *Engraulis mordax*. Only one live-bait sportfishing boat operated in 1962 and 1963, but by 1965, live-bait fishing for striped bass was firmly established (McKechnie and Fenner, 1971; Chadwick and Albrecht, 1965).

Ocean surf-casting methods also changed in the mid-1960's when it was discovered that striped bass gathered in feeding schools at certain areas off ocean beaches, at which time they would readily take artificial lures cast from shore (Miller, 1974). Until then, practically all surf-caught bass were taken with bait, usually clams. According to Frey (1971), by 1966 nearly all striped bass surf anglers had switched to metal and plastic artificial lures. This changeover also affected the catch along ocean beaches of redbait surfperch *Amphistichus rhodotus*, which previously had been taken incidentally on hooks baited for striped bass. When anglers switched to lures cast out and quickly retrieved, redbait surfperch (which are seldom taken by this method) occurred much less frequently in the catch (Frey, 1971).

Today in San Francisco Bay, live-bait fishing is the primary method used by striped bass sportfishing boats at the height of the summer and fall seasons. Anchovies and shiner perch *Cymatogaster aggregata*, are used as bait. Boats repeatedly drift over areas where an abrupt change in depth occurs and when the current is running swiftest. In early spring, however, some will troll deep, using either single lines rigged with plastic skirt lures ("hoochies") or tandem spreader rigs baited with artificial lures (spoons, plugs, bug-eye

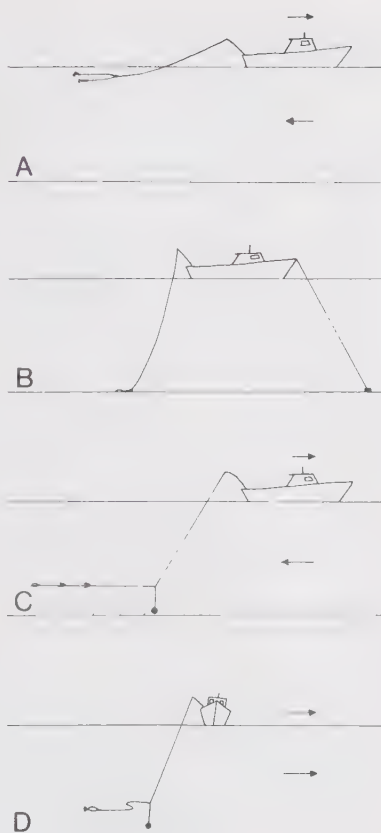


Figure 4.—Over a span of about 8 years, striped bass sport fishing boat methods have changed from (A) near-surface trolling and (B) bottomfishing, to (C) deep trolling and then (D) deep drifting with live bait.

jigs). Among the advantages of live bait fishing on passenger boats, as opposed to deep-line trolling (still a very effective method), are that many lines can be fished at a time, and more anglers can be accommodated per trip. The method is also relatively simple for the novice angler (C. Anfrinson, Captain, fishing vessel *Bass Tub III*, pers. commun.).

In San Pablo Bay and adjacent bays, rivers, and sloughs and up into the Delta, bait fishing remains the most widely used method in fall and winter. Staghorn sculpin *Leptocottus armatus*, mudsuckers *Gillichthys mirabilis*, and bay shrimp *Crangon* sp.,

are used as bait. During the summer, anglers will sometimes troll artificial lures.

Private boat and rental skiff anglers throughout the bay system conduct both surface and deep-line trolling for bass as well as plug casting and bait fishing. Shore anglers cast baits and artificial lures from piers, jetties, banks, and beaches. Some fly-fishing is done in the relatively shallow, quiet waters of the bay.

Boat rods and revolving spool reels are generally used for deep trolling and deep drifting with live bait, while both spinning and conventional tackle are used for surface trolling and casting. Fiberglass surf-casting rods range up to 12 feet (3.7 m) long. Line strengths vary with fishing method, usually anywhere from 12 to 20 pound test monofilament for casting, to 40 pound test or heavier for deep-line trolling where cannonball sinkers (1/2- to 1-pound or 0.2- to 0.5-kg) are used. In deep-line trolling, some sportfishing boats use heavy duty monel wire for the main line, where 2- to 3-pound (0.9 to 1.4-kg) sinkers are needed to carry the long (up to 12 m) monofilament leader to the desired depth.

Sturgeon Fishing in San Francisco Bay

Sturgeon fishing, prohibited by law in 1917, was opened to sportfishing in 1954; the fishery centered in the San Francisco Bay estuary system. The most common species, the white sturgeon, *Acipenser transmontanus*, reaches a length of 20 feet (610 cm) and a weight of 1,800 pounds (816.5 kg) (Squire and Smith, 1977). A size limit of 40 inches (102 cm) was established with a one-fish bag limit. Initially, snagging by trollers seemed to be the only effective method, but trolling for sturgeon was prohibited by law in 1956 (Miller, 1972). Relatively few fish were taken until 1964 when it was discovered that bay shrimp, *Crangon* sp., was a very effective bait (McKechnie and Fenner, 1971). With this discovery, yearly sport fishing boat catches jumped from 3 sturgeon in 1963 to 2,400 in 1967—a striking example of the effect of a new fishing technique on

a fishery. There seems little doubt that angler efficiency increased over this period.

In succeeding years, bottom fishing for sturgeon became increasingly popular in the San Francisco Bay area, with most angling taking place from sportfishing boats and skiffs (private and rented) in San Pablo and Suisun Bays from fall through early spring. In these areas the standard equipment is a 7- to 8-foot (2.1- to 2.4-m) boat rod with a flexible tip, and conventional star-drag reel loaded with about 300 yards (274 m) of 40- to 50-pound test monofilament line. Most anglers use one of the commercially available sturgeon rigs that include a wire or heavy sleeve, and hooks. The bait is usually live or freshly-dead bay shrimp (Fig. 5), although mudsucker, *Gillichthys mirabilis*, and ghost shrimp, *Upogebia pugettensis* and *Callinassa californiensis*, have also been used in recent years. In fact, the use of callinassid bait has increased dramatically since about 1976, and it is possible that ghost shrimp, particularly *C. californiensis*, may be an even more effective bait for sturgeon than bay shrimp.

Sinker weights vary with the strength of the current. The method is to locate a known or suspected sturgeon ground, then anchor. After dropping a baited hook over the side, line is payed out and the rod tip watched closely. After the first light tap, a few more feet of line is payed out. Usually when the second tap is felt, the angler sets the hook. A modest fishery takes place in south San Francisco Bay, where anglers use methods and tackle similar to those in San Pablo and Suisun Bays.

A separate fishery also exists in upper San Francisco Bay during the herring (*Clupea harengus*) spawning runs that occur from about January to March. At this time, sturgeon are known to feed on herring eggs around the Sausalito and Tiburon Peninsulas, where, during the height of the runs, sturgeon are caught by shore and boat anglers (Fig. 6). This fishery developed over the past 8 years, growing from a handful of anglers in 1970, and increasing rapidly since 1974 as more anglers learned of the availability of

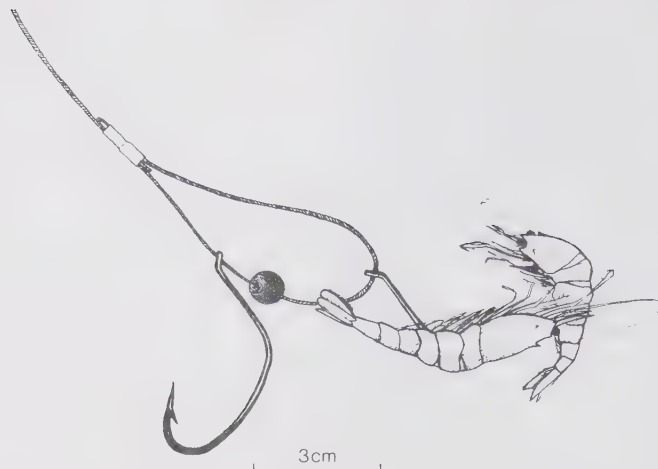


Figure 5.—Discovery in the early 1960's of bay shrimp, *Crangon* sp., for bait revolutionized the sturgeon fishery in San Francisco Bay. The terminal end of a typical rig is shown (one hook left unbaited to show hook type).



Figure 6.—Landing a white sturgeon in San Francisco Bay. In recent years, Bay anglers have developed effective methods for catching sturgeon on the herring spawning grounds near the Golden Gate Bridge.

sturgeon in these areas and the techniques to catch them (L. Green, San Bruno, Calif., pers. commun.). The fish are caught bottom fishing close to shore, often during swift-running incoming tides. Instead of the standard grass shrimp, herring fillets or wads of herring roe are used for bait. In the herring spawning areas, the sliding sinker rig is used over sand or mud bottom, while over rocky bottom the

weight is attached to a short length of lighter line which is tied to a swivel about 60 cm above the hook.

Recently, snagging again became a problem, especially during times when sturgeon would congregate to feed on herring spawn. Reportedly, some anglers were casting out heavy lures and snagging fish on the retrieve. In 1978, this type of snagging became illegal, and anglers are now required to

return to the water all sturgeon not hooked in the mouth.

Ocean Salmon Fishing

Ocean fishing for salmon was started by recreational anglers in Monterey Bay in the early 1880's. According to Scofield (1956), they trolled for salmon from small sailboats using two hand rods and a line over each side equipped with a hook and leader. Some lines were provided with two leaders and hooks. The leader was about 30 feet (9 m) long and carried a lead sinker midway between the main line and lure. Up until this time, salmon had been taken only in rivers and bays by commercial netters and in rivers and streams by anglers using fly-fishing or freshwater baitcasting tackle.

By 1893, the troll-line sport fishery had become well established in the Monterey Bay area. Anglers fished from sailboats or rowboats using "stout lines and hooks attached to flyrods or simply fished by hand . . ." (Smith, 1895). Sardine was the principal bait. In 1893, a writer for *Forest and Stream* (predecessor to today's *Field and Stream* magazine) reported fishing for salmon in Monterey Bay with a trolling rod, multiplying reel, and linen line (cited by Smith, 1895).

By 1902, anglers were trolling for salmon in the ocean just north of San Francisco. According to old newspaper reports, they trolled from launches, fishing the area between Tennessee Cove and Bolinas Bay, Marin County, some using artificial lures (Neal, 1977). Around the same time in Monterey Bay, anglers apparently were still relying on sardines, *Sardinops sagax*, for bait, and spoons were only rarely used (Jordan and Evermann, 1902). They would use a 30-ply line and a 3- to 5-pound (1.4- to 2.3-kg) sinker attached to a lighter 24-ply line, 6 m above the hook. About 150 feet (46 m) of line would be let out and the bait fished 6-15 m below the surface, trolled at about 4 miles per hour (Jordan and Evermann, 1902).

By 1908, ocean salmon anglers in central California were beginning to use lighter, more sporting tackle for salmon. That year, large catches of salmon were reported in Monterey

Bay, landed by anglers using light rods, 9-thread line, and size 7/0 hooks baited with smelt, anchovy, or sardine (Holder, 1908). In 1908, a writer for *Forest and Stream* reported that while "most professional salmon fishermen [off San Francisco] use sardines and a heavy sinker on thick line, the amateurs use a new trolling spoon on a light line, and secure many more strikes" (A.P.B., 1908).

According to Croker (1938b), very little salmon angling took place in the ocean north of Bodega Bay until after World War II, although sometimes north coast commercial trollers would allow anglers on their boats. The technique of "moocking" for salmon was introduced to California at Humboldt Bay in the late 1930's or early 1940's, when there was a great influx of anchovies into the Bay (D. Gotshall, Calif. Dep. Fish Game, Monterey, Calif., pers. commun.). This method apparently originated in the Seattle, Wash., area, developed by Elliot Bay anglers around the turn of the century (Haw et al., 1967).

Humboldt Bay moocking involves drifting a bait (usually anchovy) close to the bottom on an incoming tide, repeatedly lifting the bait up at an angle, then letting it drop back again. The action is also imparted by varying the boat speed (motor or oar power), to help the drift when the current is running swiftly. Moocking rods are usually longer, lighter, and more limber than conventional rods used in ocean trolling for salmon, and are combined with revolving spool reels. The line (after about 1950, nylon monofilament) is usually weighted with a light, crescent-shaped sinker.

In the San Francisco area in the 1930's, metal sinker releases (the spring-loaded type similar to that used today) had already come into use. It is not known exactly when this device was introduced in California, but apparently it was first used with window sash weights, then cannonball sinkers. It soon became part of standard trolling tackle. During the 1930's, San Francisco salmon trollers would use spoons in spring, then later in the season switch to bait (anchovies, sometimes sardines). They used primi-

tive long-shank commercial salmon hooks with no eye, and these were tied directly to the cuttyhunk line, which anglers would often mark with paint or nailpolish to better gauge the fishing depth (A. W. Agnew, Sunset Line and Twine, Petaluma, Calif., pers. commun.). After the war before monofilament nylon came into use, piano wire was used as leader material (E. Neal, *San Francisco Examiner*, pers. commun.).

During the 1950's, ocean salmon fishing increased phenomenally, and no doubt the development of more powerful and dependable boat engines and improvements in boat design had much to do with the expansion of the sport (Wendler, 1960). Anglers could reach fishing grounds that were previously unsafe or out of reach. Availability of moderately priced, quality fishing tackle—fiberglass rods, monofilament line, and trouble-free fishing reels—also played a part in the expansion of ocean salmon fishing.

Today, sport fishing for salmon is conducted all along the central and northern California coast from Avila Beach to Crescent City. Most fishing north of Fort Bragg is conducted from skiffs, although commercial sport fishing boats are available seasonally at Eureka, Trinidad, and Crescent City. The majority of salmon sport boats operate out of the San Francisco Bay area. Both chinook, *Oncorhynchus tshawytscha*, and coho, *O. kisutch*, salmon are taken, with chinooks dominating the catch south of Fort Bragg and cohos entering the catch more frequently to the north. Although the tackle has changed considerably over the years, the method of fishing is basically the same used back in 1902 at Monterey Bay—trolling whole fish baits from 6 to 18 m below the water's surface, depending on where the fish are feeding.

Offshore of the Golden Gate Bridge, where the most consistent salmon runs occur, the standard tackle consists of a conventional fiberglass boat rod (7-8 feet or 2.1-2.4 m) combined with a medium-sized star-drag reel loaded with about 200-250 yards (183 to 229 m) of 20 to 30 pound test nylon monofilament or Dacron line. Many anglers

use a metal sinker release and cannon-ball weights of 1-3 pounds (0.5-1.4 kg). Plastic diving planes are sometimes used but as yet are not as common as the sinker release rig. An increasing number of boats are equipped with downriggers to carry the bait to the desired depth. Standard bait is fresh-frozen anchovy, though herring is also used. The bait is usually threaded on one of the commercially available bait holders (crowbars, easy-baiters). A sliding two-hook rig is used along the north coast, as are mooching rigs and the combination of a #2/0 hook and crescent or torpedo-shaped sinker. Some anglers attach a spinning "flasher" or wobbling "herring dodger" (both shiny metal attractors) between the sinker and bait (Fig. 7). Most north coast sport fishing boats use the flasher or dodger rig; it is not as common on San Francisco boats. Artificial lures (particularly spoons) are in use, especially from Monterey south to Avila Beach, but in general these run a distant second to fish bait.

Boats troll over a known fishing ground at about 2 to 5 miles per hour with lines fished at slightly different depths to avoid tangles. Coho salmon are taken nearer the surface than chinooks, with baits fished usually no deeper than 6 or 9 m below the surface.



Figure 7.—Salmon trolling rig showing cannonball sinker and release, metal attractor, and rigged anchovy.



Figure 8.—Sport boat seining for sardines outside Long Beach Harbor, 1928. In the early days of southern California live-bait fishing, sport boats netted their own bait before picking up passengers (long bamboo poles rest against cabin). (Photo courtesy of California Department of Fish and Game.)

Southern California Live Bait Fishing

As mentioned earlier, live-bait fishing from public sport fishing vessels was introduced in southern California in the 1920's. Initially, trolling was the principal method, but as early as 1925 some boats were using live bait. These early "live-bait boats" would go out on a scheduled basis every day, but were primitive and offered anglers little in the way of comfort (Davis, 1949). Bait was kept in barrels which had to be replenished every few minutes with buckets of fresh seawater (Hull, 1973). Sardines, the principal live bait, were netted prior to the fishing trip (Fig. 8).

In the 1930's, the use of live bait for both bait and chum became established (Fig. 9). By the mid-1930's, a few boats began to specialize in catching and



Figure 9.—Live-bait fishing off Rocky Point, southern California, 1938. (Photo courtesy of California Department of Fish and Game.)

supplying live bait to others, and the live bait industry was born (Hull, 1974). Also, new live bait tanks were

developed that circulated a continuous flow of pumped water to keep the bait in good condition. Standard tackle was



Figure 10.—Deck hand gaffs a bluefin tuna on a 1937 fishing trip off Catalina Island. In the late 1930's, southern California live-bait anglers fished with hefty cane rods, star-drag reels, and linen line using sardine for bait and chum. (Photo courtesy of California Department of Fish and Game.)



Figure 11.—Live-bait fishing off southern California in the 1970's. Modern sport boats such as this one are faster, safer, and more comfortable than those of prior decades, and are outfitted with sophisticated electronic fish-finding, radio, and navigational equipment to more efficiently locate concentrations of fish.

a bamboo rod, star-drag reel, twisted linen line (cuttyhunk), and a gut or wire leader (Fig. 10).

In the years that immediately followed World War II, most sport

fishing boat anglers were still using medium star-drag reels, Calcutta bamboo poles, twisted linen (and some twisted nylon) line (27- to 30-pound test), and live bait hooks in sizes 1/0

through 4/0, depending on target fish size. Sinkers (most often the torpedo-type), were used for California halibut, *Paralichthys californicus*, and other bottomfishes. Many anglers were now using plastic spools on their reels to make it easier to cast live baits. Leader material was either gut or piano wire. Heavy stainless steel wire was often used for jigging, and some anglers, nicknamed "feather merchants," would bring lighter tackle and fish with feather jigs. By the late 1940's, anchovies had pretty much replaced the hardier sardine as live bait, as the latter were getting too difficult to obtain. Sometimes queenfish, *Seriphus politus*, was used as live bait for kelp bass, *Paralabrax clathratus*, and California halibut.

During the 1950's, soft monofilament nylon line began showing up on sportfishing boats, and fiberglass rods were replacing the old cane rods. New high-speed retrieve reels (star-drag type) were introduced in 1959, and became popular for yellowtail, *Seriola dorsalis*, jigging (H. Heerse, Penn Reels, Philadelphia, Pa., pers. commun.).

In the 1960's and 1970's, fiberglass rods and nylon monofilament line came into widespread use on sportfishing boats (Fig. 11). Today, live bait anglers usually use light to medium action fiberglass rods, generally from 6½ to 7½ feet (2.0 to 2.3 m) long and with a fast taper. These live-bait rods are designed to be strong yet light, with tips flexible enough to cast a small live anchovy on an unweighted line. The choice of medium or light tackle depends on the species sought, and often how crowded the boat is. If many anglers are fishing at close quarters, light tackle is usually discouraged. Open faced spinning or conventional star-drag reels are used, loaded with about 250-300 yards (229-274 m) of 15- to 20-pound test monofilament line. Today, live-bait hooks are much smaller than those used throughout the postwar years and are of the short-shank O'Shaughnessy type with point bent toward the shank (Garrison and Rice, 1972). Generally, hook sizes range from 1 through 6, and the hook is tied directly to the end of

the line. If the fish are not near the surface, a lightweight rubber-cored sinker is attached to the line about 3 feet (91 cm) above the bait (Fig. 12). Live bait is still predominantly anchovy, which is hooked upwards through the gill collar or through the snout. Larger baits and larger hooks (sizes 1/0 to 4/0) are used for bigger game such as large white seabass, *Cynoscion nobilis*, yellowtail, and large kelp bass. Live squid (*Loligo* spp.), hooked through the tip of the mantle, is prime bait for the above species. Pacific mackerel, *Scomber japonicus*, usually hooked through the snout, is also used as live bait for these larger fish. Queenfish, hooked under the breastbone, is still popular for large kelp bass.

A sport boat will arrive at a known fishing spot, such as the seaward side of a kelp bed, and begin to chum slowly with live anchovies, while making a circle about 46 m in diameter. If fish begin to break the surface within the circle, the captain will anchor the boat and continue chumming (Fig. 13). Anglers then cast or ease their baited hooks over the side, set their reels in free spool or open bail, and allow the bait to move relatively free in the water. When a game fish takes the bait, it is permitted to run a short distance before the reel is put in gear and the angler sets the hook.

Offshore Bottomfishing in Northern California

For many years, offshore bottomfish have been an important staple of California marine recreational fishing. Rockfish (*Sebastes* spp.) are the principal species in the bottomfish catch, although others, such as lingcod, *Ophiodon elongatus*, cabezon, *Scorpaenichthys marmoratus*, and flatfishes, also are landed. Approximately 55 species of rockfish occur in California waters, and 29 of these are known to occur in the northern California sport boat catch (Miller and Gotshall, 1965). Since the early 1960's, rockfish have ranked first in numbers of fish taken by sport boat anglers, and between 1972 and 1975 they composed over one-half of the annual statewide

catch (Pinkas, 1977). Rockfish are important in both northern and southern California, and are particularly valuable in areas where other game fishes show up less predictably or only seasonally.

Offshore bottomfishing for sport has been conducted in California since before the turn of this century. According to early newspaper reports, in the late 1870's and 1880's there were sport-fishing excursions during summer out of Humboldt Bay to bottom fishing grounds off False Cape and Cape Mendocino (Wainwright, 1965). Two steam tugs, each accommodating about 30 passengers, operated out of the Eureka area; and tickets for a fishing trip were sold to anglers for \$2.00 each (Wainwright, 1965). Rockfish composed the bulk of the catch, though Pacific halibut *Hippoglossus stenolepis*, and true cod (*Gadus macrocephalus*) also were taken. The reports do not go into detail about tackle, but the anglers apparently used handlines, the primary method used for ocean bottomfish in California for about 50 years thereafter.

By the 1930's, rod and reel was beginning to appear in the ocean bottomfishery, although most fishing was still done with handlines. In 1933, a pleasure fishing trip out of Princeton was described by Buchanan (cited by Young, 1969). According to his report,

14 anglers boarded a 30-foot (9.2-m) long fishing launch and went out one-half to three-quarters of a mile offshore before dropping lines. Only two anglers used poles, the rest used handlines with three hooks baited with sardine, the whole rig weighted with a 2-pound (0.9-kg) sinker. Black rock



Figure 12.—Southern California live-bait rig. Rubber-cored sinker (above bait) is used if fish are not feeding near the surface.



Figure 13.—Live-bait fishing from a southern California sport fishing boat.

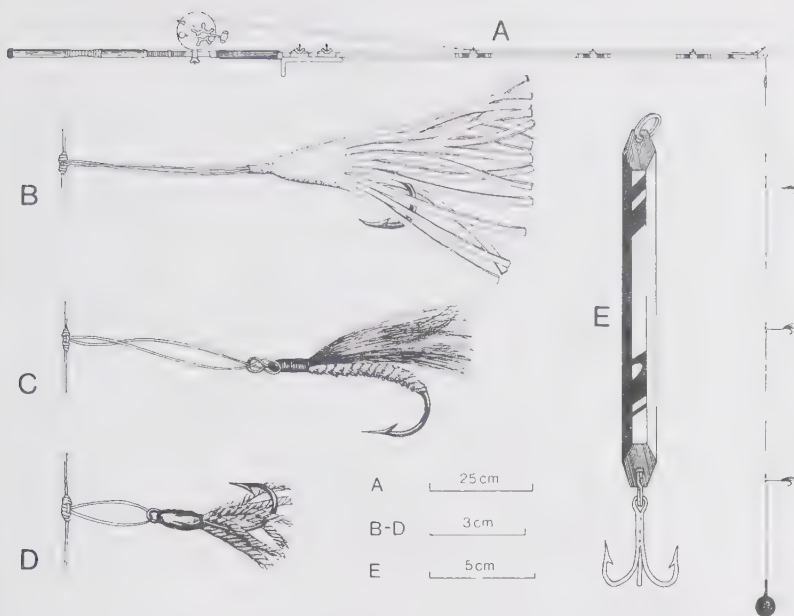


Figure 14.—Northern California bottomfish tackle (1970's): (A) Boat pole with star-drag reel, deck plate, multijig rig, and cannonball sinker; (B-D) variations in rockfish jig designs; (E) chrome "hex" jig used for lingcod and large rockfish.

fish (assume *S. melanops*) dominated the catch, although flatfishes and other species of rockfish were also taken.

In Monterey Bay, offshore bottom-fishing up until the early 1940's was done almost exclusively with cotton handlines, which were supplied to anglers at the onset of the trip (F. Arcoleo, retired sport boat captain, Monterey, Calif., pers. commun.). Each handline was about 91 m long, rigged with two dropper lines and 5/0 hooks baited with salted sardine, and weighted with an old railroad spike. Around 1941, Monterey sport boat anglers began using bamboo poles, star-drag reels, and twisted linen (cuttyhunk) line. The standard method was baitfishing with sardine, although some anglers (usually the more experienced ones) used chrome hexagonal jigs for blue, olive, and yellowtail rockfish. These 24-ounce (0.68-kg) "hex" jigs were, and still are, very effective but it takes skill to avoid snagging and losing them on the bottom.

In the late 1940's, fiberglass rods began showing up on the sport boats

and squid was rapidly replacing sardine as bait. The first fathometers also came into use in the late 1940's, but they were generally not accepted until after 1955 when more sensitive models became available. The new monofilament nylon line also took a while to be accepted because even though it was lighter and drifted less than linen line, it stretched badly and damaged plastic reel spools that were used in bottom-fishing at the time. About a decade later, when metal spools were used, and line manufacturers were able to cut down on line stretch, nylon monofilament replaced linen line in the Monterey fishery.

Around the time nylon monofilament line was being accepted, an important change in terminal tackle occurred with the introduction of the multiple jig rig for rockfish. These rigs, which vary in design from port to port and are variously called "cod flies," "shrimp flies," "wonderlures," etc., consist of a 5-foot (152-cm) nylon monofilament leader with from three to five hooks on short dropper loops the hooks decorated with brightly

colored yarn, synthetic fibers, or plastic skirts (Fig. 14). According to sport boat captains in Monterey Bay, when these rigs were introduced in the Monterey area around 1957, the boat that first used them consistently caught more fish than other boats fishing in the same area at the same time. Soon afterward, other sport boat operators in the Monterey Bay area began to use the new multijig rigs. According to Miller (Calif. Dep. Fish and Game, Monterey, Calif., pers. commun.), rockfish landings increased during this period, especially catches of schooling pelagic types such as blue, yellowtail, widow, and olive rockfishes. In this instance, the new type of terminal tackle may not only have affected catch-per-unit-of-effort, but species composition of the catch as well. Also, in the late 1960's and early 1970's spinning gear became available on the Monterey boats so that anglers could fish with feather jigs in case a surface feeding school of blue or yellowtail rockfish was found.

The multijig rockfish lures are now commonly used throughout most of northern California, along with the standard combination of fiberglass boat rods, heavy duty star-drag reels, and nylon monofilament and braided Dacron lines testing at 40-60 pounds. The multijig rigs are fished successfully with or without bait (squid or cut anchovy). Sinker weights vary from 8 ounces to 2 pounds (from 0.2 to 0.9 kg) or more. The hexagonal chrome jigs, in use before World War II, are still commonly used, especially for lingcod, which are also taken with single hook rigs baited with small live rockfish and live squid when available. Recently, other types of jigs, some very similar to the "candy bar" types used on southern California sport boats, have been introduced to central California bottomfishing.

Even if it is assumed that the fishing power of the terminal tackle itself has not changed, ongoing improvements in electronic equipment and boat and engine design since the 1940's have obviously enabled boats to fish in deeper water and travel to new bottom-fish grounds farther from port. Ultra-sensitive fathometers have helped to

locate new reef areas and concentrations of fish with less search time and greater accuracy. The switch from handlines to rod and reel and lighter line also made it easier to fish in deeper water. Today boats are able to fish in water to 183 m deep, whereas handline depth averaged about 37 to 46 m, and early rod and reel depth about 73 to 92 m.

When handlines were used, boats could only fish in shallow water because the heavy lines drifted badly in the current and even with relatively short lengths of line, there was a constant problem with on-deck line tangles between pulls, which cut down on actual fishing time. On some boats, large wooden reels that clamped to the deck rail were used to haul up line, but not all anglers used them, and they were cumbersome and offered little in the way of sport. With rod and reel came lighter line (first linen and then even lighter nylon monofilament and braided Dacron), and soon line drift was no longer much of a problem. Since excess line was retrieved on the reel spool, the major cause of on-deck line tangles was eliminated. Other developments over the past 10 years, such as deck plates³ and reel handle extensions, have also made it easier to crank up fish and heavy sinkers from the decks.

Discussion

It is often said that most of the fish are caught by a small minority of anglers—the ones with the most experience and skill. Although these two factors are obviously important, for every expert there are thousands of average anglers and growing numbers of novice anglers. It is likely that the development of efficient, well-made, yet moderately priced tackle that is simple to operate and maintain has tilted the odds in the average anglers' favor over the years, and will probably continue to do so as new, even

more advanced fishing equipment is developed.

Although there are few quantitative data on the relative efficiency of old versus new gear, it is obvious that saltwater fishing equipment has definitely changed, with the most dramatic developments occurring after World War II. The postwar years were also a time of rapid and tremendous growth in California. Between 1940 and 1970, the State's population tripled and so did the per capita income of its people. More spendable income and more leisure time undoubtedly contributed to the saltwater angling boom in California, and to an increased demand for angling products and services and better dissemination of angling information.

Changes in fishing methods, as well as tackle, also have been observed in saltwater sport fishing in California (Fig. 15). In just 8 years (1957-65), striped bass sportfishing boat methods in San Francisco Bay changed from bait fishing to deep-line trolling to live-bait drifting. Within only a few years, ocean surf casters, who had for years still-fished with bait for striped bass, switched to casting artificial lures. The sturgeon fishery received a tremendous boost when, in the 1960's, grass shrimp was discovered as an effective bait. In the 1970's, the development of successful methods to catch sturgeon on the herring spawning grounds essentially opened up a new fishing area for this species in San Francisco Bay. Multijig terminal tackle has largely replaced the standard bait rig in offshore bottom-fishing in northern California. Development of lightweight synthetic fishing lines, dependable fishing reels and rods, and improvements in boat design and equipment have all changed the style of marine sport fishing in California. No doubt many other California recreational fisheries not mentioned in this report have been similarly affected by changing methods as well as by new kinds of tackle.

Because angler efficiency may also be altered when such changes occur, these factors should be considered when biologists assess relative abundance using catch-per-unit-of-effort data. Changes in methods or tackle

may not only affect the catch of target species, but also that of incidentally caught species.

Ideally, information on relative efficiency should be obtained when a fishery undergoes significant changes in gear or methods, but if this is not possible, these changes should at least be monitored as closely as possible and taken into account when estimating, through effort units, relative abundance of marine game fish populations.

Acknowledgments

Without the cooperation and advice of those I interviewed—veteran anglers, members of the tackle industry, sport boat skippers and others connected with the marine recreational fishing industry—this chronology would not have been possible. I am also grateful to Norm Abramson, Arthur Agnew, Charles Davis, Jr., Roger Green, Daniel Miller, Ed Neal, and George Reiger for reviewing the manuscript and offering many helpful suggestions. Joe Lesh and Dan Gotshall helped by providing needed information on north coast salmon fishing.

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³A plastic or metal plate clamped on the lower part of the rod shaft and rested on the boat railing for better leverage when reeling in.

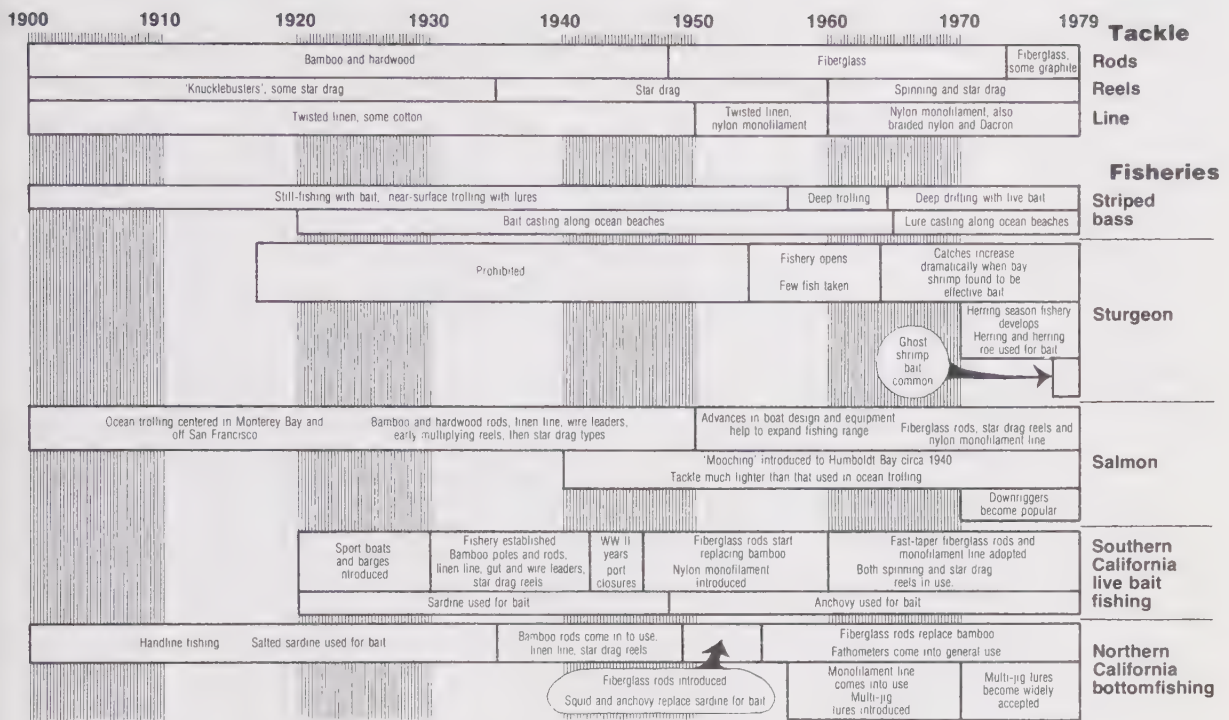


Figure 15.—Chronology of some changes in saltwater angling methods and gear in California. (Demarcation lines for changes are approximate.)

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THE FISHERIES OF SAN FRANCISCO BAY: PAST, PRESENT AND FUTURE

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The character of the important fisheries of San Francisco Bay (chinook salmon, striped bass, sturgeon, shad, Pacific herring, northern anchovy, starry flounder, surfperch, elasmobranchs, bay shrimp, and bivalves) has changed dramatically over the past century. Many commercial fisheries that were once important to the Bay Area economy have disappeared (e.g., the river fishery for chinook salmon and the extensive clam and oyster industries), and although other commercial fisheries have been revived in recent years (e.g., herring, bay shrimp), there has been an overall change in emphasis from commercial to recreational fishing. This has been largely due to legislation restricting the commercial harvest of anadromous species such as salmon, striped bass and sturgeon.

Man-induced changes in the environment are implicated in the decline of certain fishery resources. Water storage and diversion projects have affected the distribution and abundance of salmon and striped bass, and land reclamation and domestic sewage pollution essentially eliminated the clam and oyster industries. Fishing pressure has also been linked with the decline of the bay shrimp and sturgeon fisheries.

The San Francisco Bay-Delta region (Fig. 1) was once the foremost fishing center on the West Coast but has long since relinquished this position. Extensive land reclamation, dredging, water pollution, and water development projects have taken a great toll on the habitat, and overfishing can also be blamed for much of the decline. Fishery resources came under heavy exploitation between 1870 and 1915, and many fishery products from within the Bay began to decline even before the turn of the century (Skinner 1962). Introduction of new species has mitigated part of the damage, although the full ecological effects of these introductions are not known.

On the positive side, public concern and subsequent investigations by the California Department of Fish and Game (DFG) and other state and federal conservation agencies have led to restrictions which have at least slowed the destruction of habitat and fishery resources. These resources include a wide variety of fish and shellfish, some important to recreational interests, others valuable as commercial products, and still others waiting for the right circumstances to be utilized. Over 100 species of elasmobranchs and fishes, some 70 bivalves and 30 decapods have been recorded in the rich fauna of the Bay-Delta region (Painter 1966; Messersmith 1966; Aplin 1967; Green 1975; Eldridge 1977; unpublished catalog of invertebrates, Calif. Acad. of Sci., San Francisco).

The following sections describe the history and current status of the commercial and sport fisheries that have existed within the San Francisco Bay-Delta complex. Emphasis is placed on the changing nature of the fisheries—how they have been affected by demand, resource availability, regulations, and in particular, alteration of the environment by man. Species life history information, where pertinent, is also presented. Those covered are native and naturalized exotic species—we have not attempted to cover the extensive oyster industry which existed from 1870 to the late 1930's, mainly because the species that largely supported the industry, the eastern oyster

SAN FRANCISCO BAY

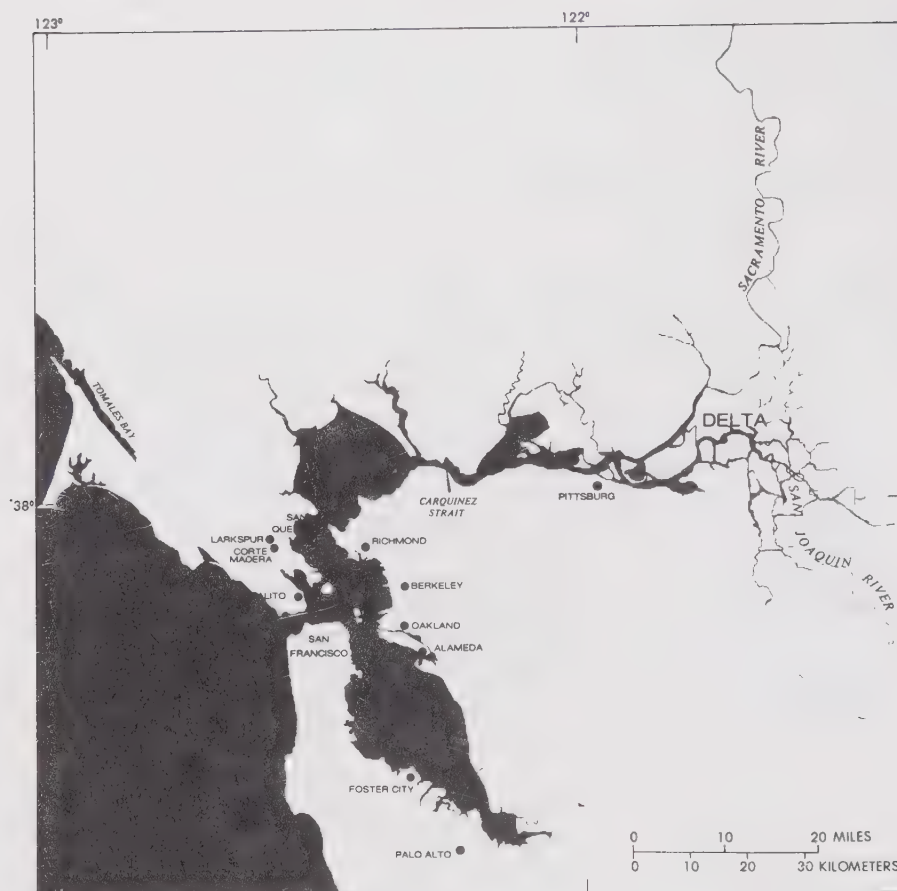


Fig. 1. Index map of the San Francisco Bay-Delta and environs.

(*Crassostrea virginica*), was imported for seed culture or holding only and never became successfully established in the Bay. It should be mentioned, however, that the San Francisco Bay oyster industry was at one time the single most valuable fishery in the state; it declined rapidly after the turn of the century as water quality deteriorated and conditions became unsuitable for oyster culture. The market crab (*Cancer magister*) also supported a valuable fishery in the San Francisco area, but is not covered here because of the lack of quantitative information on the early fishery inside the Bay prior to the time when crabbing operations moved outside the Golden Gate. The Bay, however, is an important nursery area for this species (see Tasto 1979).

Skinner (1962, 1972a, b) has provided excellent reviews of the history and current status of the fisheries of San Francisco Bay area. This chapter summarizes and updates these and other works and provides additional insight as to the possible fate of the fisheries resources in the future.

CHINOOK SALMON

The chinook salmon, *Oncorhynchus tshawytscha*, is an extremely valuable food and game

resource in the Bay area and along the entire northern California coast. About 80% of all California's chinook salmon landings originate from stocks in the Sacramento-San Joaquin river systems (Skinner 1962). Most recreational fishing and all commercial fishing for chinook salmon now takes place outside the Golden Gate.

The chinook salmon attains a length of 147 cm and a weight of 57 kg, and its ocean range extends from San Diego, California, north to the Bering Sea and south along the Asiatic Coast to northern Japan (Fry 1973).

The species is anadromous, passing through the Bay and ascending rivers (Fig. 2) to spawn in cool, fresh-water streams over clean gravelly substrate (Fry 1973). Like all Pacific salmon, the

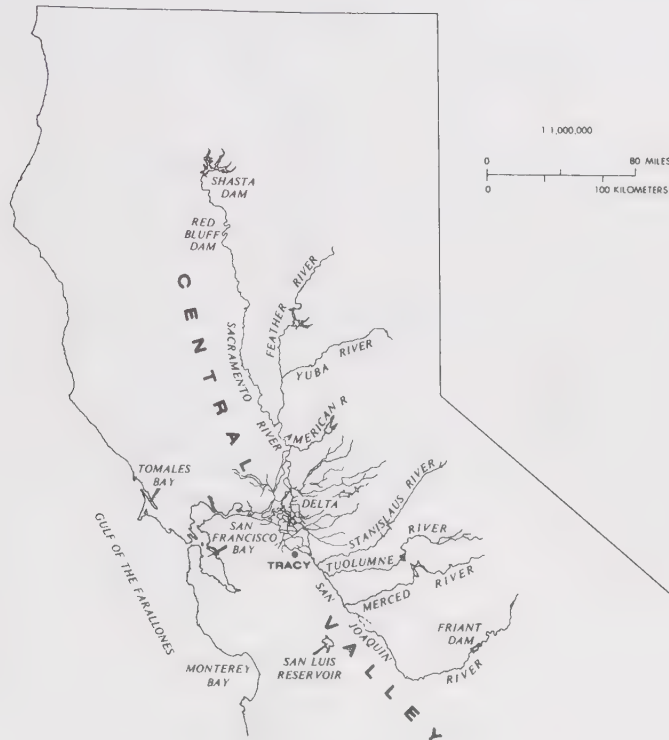


Fig. 2. The drainage basin of the San Francisco Bay-Delta system.

adults die after spawning. Eggs hatch in 50 to 60 days, and about a month later the young emerge from the gravel (Fry 1973). Peak downstream migration of young occurs in the spring and to a lesser extent in the fall. Fingerlings from 2 months to 1 year old move downstream through the estuary into the ocean, where they remain from 1 to 4 years (usually 3) to grow and mature before returning to native spawning streams (Heubach 1968).

There are at present three different stocks in chinook salmon in the Central Valley; these stocks are named for the time each enters spawning streams—spring-run, fall-run, and winter-run fish (Jensen 1972). A fourth group (late fall-run) has been identified (Hallock 1977), but we have included this group in the fall-run category. Most spring-run fish spend the summer in deep pools

SAN FRANCISCO BAY

and do not spawn until the fall. Fall-run fish spawn soon after their arrival on the spawning grounds, and winter-run fish spawn in late spring and early summer (Hallock 1977; Jensen 1972).

Fall-run salmon are by far the most numerous and support the bulk of ocean sport and commercial fisheries. These fish spawn predominantly in the Sacramento and its tributaries, though some enter San Joaquin tributaries such as the Stanislaus, Merced, and Tuolumne rivers (Fig. 2). According to Jensen (1972), winter-run fish, which ascend the Sacramento system, have in recent years become the second most numerous group. Slater (cited by Heubach 1968) believes these fish are descendants of a small run that spawned in the McCloud River, a tributary of the Sacramento that was blocked off to spawners after construction of Shasta Dam. The spring run, which was apparently quite extensive prior to the construction of Shasta and Friant dams, is now the least numerous variety (Jensen 1972). Many spring-run fish formerly spawned in the San Joaquin River system, but due to inadequate flow caused by dam construction and other water projects, the Sacramento system now supports most of what remains of the spring run.

History of the Fisheries

Clark (1929), Skinner (1962) and Scofield (1956) provide good background information on the history of the salmon fishery. According to these authors, commercial fishermen began fishing for salmon around 1850 using gill nets and seines in the Sacramento and San Joaquin rivers and in parts of Suisun and San Pablo bays.

The first salmon cannery started operation on the Sacramento River in 1854. The industry grew rapidly, stimulating the early growth of the fishery. In 1864 one cannery packed 2,000 cases of salmon, each case containing 48 one-pound (0.45 kg) cans (Clark 1929). By 1882, 200,000 cases were produced by a total of 19 canneries operating on the rivers. After that year the industry began a gradual decline and ceased operations in 1916.

Records of the total river catch (Fig. 3A), which became available after 1874, give a better indication of the magnitude of the early salmon harvest. During the ten-year period between 1874 and 1884, an average of 3,220 t (metric tonnes) was landed annually, with a peak harvest of 4,900 t in 1880—the highest catch ever recorded. Ocean trolling for salmon, later to replace the river fishery, increased steadily after the late 1890's when gasoline boat engines were introduced (Scofield 1956). The major shift to ocean fishing, which took place from the late 1920's to the early 1940's, was largely augmented by legislative restrictions that curtailed river netting, such as stream closures, closed seasons and gear restrictions (Scofield 1956). In 1957, the year of the lowest river catch on record (146 t), legislative action eliminated all commercial salmon fishing inside the Golden Gate, making the ocean troll fishery the only legal commercial salmon fishery in California.

After World War II, sport trolling for salmon came into prominence, and the San Francisco area now produces the most consistent ocean sportfishing for salmon in the state (Squire and Smith 1977). About 45% of the chinook salmon taken near San Francisco are landed by recreational fishermen (P. O'Brien pers. comm.).

Environmental Problems

It is beyond the scope of this report to enumerate all of the many man-made changes that have affected salmon populations in the Central Valley. Readers are advised to refer to Clark (1929), Skinner (1962, 1972a), Kelley (1966), Heubach (1968), and Jensen (1972) for more detailed information.

Spawning streams were already being destroyed as early as the Gold Rush days by hydraulic gold mining, railroad construction and lumbering operations. These activities left many streams badly silted or blocked by debris (Gilbert 1917). Water development, particularly storage and

diversion projects, had an immense effect on salmon stocks by blocking access to spawning areas above dams, reducing flow and altering temperature regimes below dams, diverting fish into irrigation channels, altering the natural condition of spawning streams, and, in the case of water transport projects, changing the hydrography of the Delta itself.

In 1928, before many of the major dams had been constructed, and before the advent of the federal Central Valley Project (CVP) and State Water Project (SWP), an estimated 80% of the original Sacramento-San Joaquin salmon spawning grounds had already been cut off by obstructions (Clark 1929). The construction of Shasta Dam in 1944 eliminated approximately 50% of the available spawning area of that river (Skinner 1962). Completion of Friant Dam on the San Joaquin River in the mid-1940's essentially eliminated salmon runs in the main stem of that river (Menchen 1977). Dam construction and water diversions on other rivers and streams have also blocked valuable spawning areas, or reduced flows to the extent that either the adults can not or

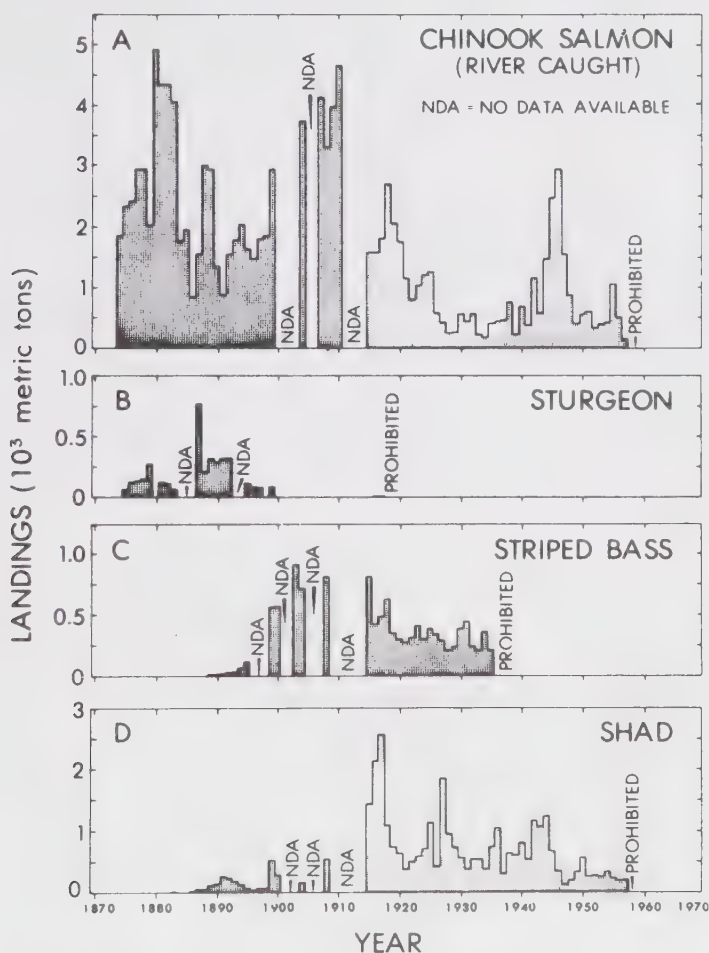


Fig. 3. Commercial fish catches of the Bay-Delta and adjacent tributary streams: (A) Salmon (1874-1957) in the Sacramento-San Joaquin rivers; (B) Sturgeon (1875-1917) in the Bay-Delta; (C) Striped bass (1889-1935) in the Bay-Delta; (D) Shad (1884-1957) in the Bay-Delta.

SAN FRANCISCO BAY

will not ascend spawning streams, or the young are unable to pass downstream during their seaward migration in spring. Hatcheries have been built to replace some of the major spawning areas lost to water development.

Since the 1950's flow reversals caused by the pumping of huge volumes of Sacramento River water across the Delta to export pumps to the south near Tracy have also created problems for chinook salmon, which depend on their olfactory senses in homing to spawning areas. During periods of reduced flows and high pumping rates, Sacramento fish are attracted to the central and southern Delta by Sacramento River water present there, and are thus delayed in their spawning migration. At the same time, San Joaquin fish have to negotiate the barrier of Sacramento River water to reach their native San Joaquin water—most of which is being delivered away from the Delta to CVP and SWP transport pumps upstream (Jensen 1972; Skinner 1972b). Screens at the pumping station are fairly efficient, but large numbers of fingerling chinooks from the San Joaquin are still lost at those sites.

It has been suggested that construction of the proposed Peripheral Canal will resolve or minimize many of these problems (see for example Gill et al. 1971); however, with or without the Canal, water demands will continue to grow in California, and careful management and control of future development in the Central Valley will play an essential part in protecting the future of this important fishery resource.

STRIPED BASS

The striped bass, *Morone saxatilis*, was first introduced to the San Francisco Bay system in 1879 when 132 juveniles, taken from a small New Jersey estuary, were shipped across country by rail and released into Carquinez Strait (Skinner, 1962). A second plant of 300 fish was made in 1882 in lower Suisun Bay. Conditions in the Sacramento-San Joaquin estuary were obviously ideal, for the species flourished beyond all expectations and now supports a valuable recreational fishery within the Bay.

Today the bulk of west coast striped bass production occurs in the San Francisco Bay estuary. The species is anadromous, migrating in winter and spring to the Delta and upstream to spawn. Information on the biology of the striped bass, population size, and environmental factors affecting the species is presented by Stevens (1979).

History of the Commercial and Sport Fisheries

Ten years after its first introduction and for 46 years thereafter the striped bass supported an important commercial fishery in the Delta area. Fish were taken with gill and trammel nets, primarily in the San Joaquin River (Skinner 1962). Between 1889 and 1915 the catch usually exceeded 454 t (10⁶ lb) annually, but catches subsequently dropped and for 20 years thereafter only twice exceeded 454 t (Fig. 3C). Growing interest in sportfishing for striped bass led to increased efforts toward conservation of the species. Finally in 1935 commercial fishing was prohibited and the resource reserved exclusively for sport use.

Until the late 1950's most angling effort took place from San Pablo Bay to the Delta, but as new fishing techniques developed and partyboat fishing upstream of Carquinez Strait diminished, San Francisco Bay proper became the major fishing area (Stevens 1977). Prior to this time most fish were caught by bait-fishing and some by surface trolling; however, it was discovered that bass could be readily taken from partyboats in north San Francisco Bay trolling deep with heavy sinkers. In addition, a winter-spring fishery developed during the herring spawning runs (Chadwick 1962). In the early 1960's another major change occurred in partyboat fishing methods with the

SMITH AND KATO: FISHERIES

introduction of deep drifting with live anchovies. Today this is the primary method used by San Francisco Bay partyboats during the height of the season in summer and fall.

Impact of Water Development

Water development in the Delta has created a variety of problems for the striped bass. Water diversions have led to loss of eggs, larvae and young fish into export canals; salinity intrusion, caused by low rainfall and increased water export, has affected spawning in the San Joaquin River; and subsequent low river flows through and out of the Delta have been associated with poor year-class survival and later recruitment to the fishery (Stevens 1979).

AMERICAN SHAD

The American shad, *Alosa sapidissima*, is another transplant from the Atlantic Coast, and like the striped bass, became firmly established within the San Francisco Bay system soon after its introduction. Shad reach a length of 76 cm and become mature at 3 to 5 years (Fry 1973; Stevens 1972).

The species is anadromous, spending most of its life at sea, the adults using the Bay only as a migratory pathway enroute from the ocean to upstream spawning areas. Most shad spawn from April to June primarily in the Sacramento River system (Stevens 1972). Formerly, shad ascended the Sacramento for 300 miles or more (Nidever 1916), but since construction of the Red Bluff Dam in 1967 (Fig. 2), most runs stop at that point (Fry 1973). Unlike salmon and trout, shad do poorly at ascending fishways, especially the more common weir and orifice type (W. Leet pers. comm.).

Stevens (1972), summarizing the work of others, reports that spawning shad appear to require fresh water, a good current, and relatively warm water temperatures between 16° to 21°C. Many adult shad die after spawning. The eggs are slightly heavier than water and are carried near the bottom by river currents until hatched. Most of the young then move downstream, leaving the Delta and passing through San Pablo Bay from September to November. Young shad feed on zooplankton, primarily cladocerans and copepods. The principal food of the adults in the Delta is the opossum shrimp, though cladocerans and copepods are also eaten. Apparently nothing is known about young shad once they enter the ocean, and little is known of the oceanic habits of Pacific Coast adult shad.

Shad are extremely delicate fish, and the slightest physical injury proves fatal. Because of their fragile nature, shad young may be less apt to survive contact with fish screening devices otherwise suitable for hardier species such as young striped bass and salmon (W. Leet pers. comm.; Kelley 1968a).

History of the Commercial Fishery

Shad were first brought to the West Coast in 1871, when 10,000 fry were introduced into the Sacramento River (Nidever 1916). Between 1873 and 1880 several additional plants were made. As early as 1879, large numbers of shad started to appear in the San Francisco market. When the first few fish began to appear, some curious customers paid as much as \$10 to \$15 for a single fish, and many shad brought from \$1 to \$1.50 per pound (0.454 kg). The novelty soon wore off, however, as shad continued to increase in numbers and began to glut the market. By 1894 the price had plummeted to 2 cents per pound. Until 1912 shad were utilized entirely by the fresh fish trade, but later a salt shad market was established in China, and practically all fish were shipped there. Shad roe was salted and either canned and shipped to the east or sold in local markets.

SAN FRANCISCO BAY

During this time practically all shad were caught in drift gill nets in upper San Francisco Bay and in the Delta.

The shad catch reached a peak of 2,540 t in 1917 (Fig. 3C), but afterward landings declined. In 1958 legislation was enacted that prohibited gill netting in inland waters and the shad fishery was eliminated. The action was taken primarily to protect salmon and striped bass caught incidentally in netting operations and not because the shad population was endangered. It would appear that since the turn of the century the commercial fishery was, for the most part, limited not by population size but by lack of demand. Even though shad has an excellent flavor and is a popular food fish on the east coast, it is not sought after to any extent in California, except by recreational fishermen.

The Sport Fishery

Recreational fishing for shad started to become popular around 1950, and since then the sport has grown considerably. In 1963 DFG estimated that 100,000 angler days were spent by fishermen seeking shad on the Yuba, American, and Feather rivers (Kelley 1968a). In recent years the main stem of the Sacramento River has become the most important fishing area (D. Painter pers. comm.).

In addition, a small "bump net" sport fishery exists in the Delta area where upstream migrants are caught in large, long-handled dip nets made of chicken wire held in the wake of an outboard motor. For some reason, only male fish are caught by this method (Stevens 1972).

No quantitative information is available on the size of the adult shad population, but it is thought to be large. At the present time DFG is undertaking tagging studies to obtain population estimates. Factors influencing the survival from egg to adult are thought to be similar to those of striped bass, although predation on shad appears to be lighter (Kelley 1968a). Maintenance of *Neomysis* sp. populations in the Delta, upon which shad depend, may be an important factor in the future as increased water demands and diversions lead to reduced outflow through the Delta, increasing the duration of salinity intrusion and altering the habitat and distribution of *Neomysis* sp. especially during dry years (Orsi and Knutson 1979).

STURGEON

Two species of sturgeon occur in the San Francisco Bay estuary, the white sturgeon, *Acipenser transmontanus*, and the green sturgeon, *A. medirostris*. The largest white sturgeon taken along the Pacific Coast was reported to be about 610 cm long, weighing 817 kg. The smaller and less common green sturgeon reaches about 213 cm and a weight of about 159 kg, but most of those that are caught are considerably smaller (Squire and Smith 1977). Female sturgeon reach maturity when they are about 12 to 15 years old, or approximately 125-140 cm in length. Males apparently mature earlier, at 10 to 12 years of age and about 112-125 cm in length (D. Kohlhorst pers. comm.).

Benthic invertebrates such as clams, small crabs and bay shrimp predominate in the diet of sturgeon; however, during the winter herring spawning runs, herring eggs are reported to account for 20 to 80% of their food. Fish, such as striped bass, herring, staghorn sculpin, and anchovy are eaten in lesser numbers (Miller 1972a; McKechnie and Fenner 1971). The opossum shrimp and the amphipod *Corophium* sp. make up the bulk of the diet of young-of-the-year sturgeon (Miller 1972a).

Tagging studies indicate that white sturgeon confine their movements primarily to the estuary, spending summer, fall and winter in the lower bays and Delta, and migrating upstream

primarily in early spring. Green sturgeon appear to spend more time in the ocean and move considerable distances along the coast (Miller 1972b).

Environmental conditions necessary for successful migration and reproduction of sturgeon are not known, and to our knowledge, spawning and embryology of California sturgeon have not been described. Sturgeon larvae have been taken by DFG in the Delta and in the Sacramento River upstream to Hamilton City (rkm 330) from March to mid-June (Kohlhorst 1976; Stevens and Miller 1970). Apparently most, if not all, of these larvae were spawned in the Sacramento River above the Delta. Catches by nets set at different depths indicate larvae are demersal.

There is concern that yolk-sac larvae coming down from the Sacramento River in spring will be vulnerable to water diversions. Recommendations have been made to prevent their being diverted with the water by providing efficient screening facilities and/or pumping curtailment (Miller 1972a). Kelley (1968b) predicted that increased net velocities in Delta channels resulting from increased water transport to the south may reduce populations of *Corophium* and *Neomysis* spp., which are important foods of sturgeon. Also, proposed reclamation or bay fill may have a detrimental effect on both juveniles and adults which feed on benthic organisms over the shallow flats of San Pablo and Suisun bays.

History of the Fishery

Before the 1870's, the sturgeon resource in the estuary was virtually untapped. Only the Chinese considered them of value, but they often utilized only the gelatinous notochord (Skinner 1962). A demand for sturgeon apparently came about when "Easterners" with a taste for sturgeon and caviar migrated to the Pacific Coast. Around the same time, the Atlantic coast supply had diminished (Skinner 1962). Furthermore, great quantities of sturgeon were in demand to feed ranch hands and labor gangs prior to 1895 (Scofield 1957).

The fishery only lasted about 30 years, but within that time the resource was heavily exploited. Initially, most fishing was conducted by the Chinese, who snagged the fish using heavy setlines with unbaited barbless hooks (Fry 1973). Gill and trammel nets took many, but such catches were usually made while fishing for other species. Green sturgeon, considered inferior as a food fish, was not sought after and brought only half the market price of white sturgeon (Smith 1895). From 1875 to 1892, landings averaged 227 t annually, while between 1892 and 1901 they ranged from about 45 to 91 t (Fig. 3B). In 1895, a law was passed protecting sturgeon during part of the spawning season, and Chinese setlining was prohibited (Scofield 1957). In 1901 the State Legislature temporarily abolished the fishery, claiming the white sturgeon to be on the verge of extinction. The fishery remained closed until 1910, when it was reopened to a limited extent but then finally abolished completely in 1917.

Kelley (1968b) suggested that hydraulic mining operations in the Sacramento system may have had as much influence on the decline of the sturgeon as did overfishing. Between 1860 and 1914 tremendous loads of mining debris flowed through the river system to the sea, affecting the benthos and probably sturgeon as well. The decline in the fishery from 1875 to 1900 occurred after 15 years of rapid and heavy bed load movement of debris down the Sacramento and accumulation in Suisun and San Pablo Bays, principal feeding areas of sturgeon. This debris passed out of Suisun Bay by 1930 and out of San Pablo Bay by 1950 (see also Krone 1979).

The taking or possession of sturgeon was prohibited until 1954, at which time DFG felt the population had sufficiently recovered to recommend opening the fishery for sportfishing only. Initially, snagging seemed to be the only effective fishing method, but this was prohibited in 1956 (Miller 1972b). Very few fish were taken until about 1964 when it was discovered that bay shrimp (*Crangon* sp.) could be used successfully as bait. Afterwards, partyboat catches jumped from three

SAN FRANCISCO BAY

sturgeon in 1963 to 2,400 fish in 1967 (McKechnie and Fenner 1971).

In recent years sturgeon angling has become increasingly popular. Although they are caught throughout the year in the upper bays and Delta, best fishing is from fall through early spring when the biggest fish are taken. There is a one-fish bag limit and 102-cm minimum size. Much of the angling takes place from boats in San Pablo and Suisun bays, where anglers still fish on the bottom using shrimp for bait. During the herring spawning runs from about January to March, sturgeon also congregate around Sausalito and the Tiburon Peninsula, where, during the height of the runs, they are caught by shore and boat anglers using herring fillets or herring roe for bait. A modest fishery exists in South Bay where anglers use methods similar to those used in San Pablo Bay.

PACIFIC HERRING

Although Pacific herring, *Clupea harengus pallasii*, are distributed along the entire U.S. west coast, they are uncommon in southern California. Within the range there are a series of intergrading populations which spawn in specific areas; tagging experiments give evidence of only limited interchange among populations (Hart 1973). Major spawning areas in California are Tomales and San Francisco bays.

Each year from about November to March large schools of herring enter San Francisco Bay to spawn, principally along the shores of Sausalito and the Tiburon Peninsula. Most herring spawn when they are two years old and about 25 cm long (J. Spratt pers. comm.). Pacific herring spawn intertidally and subtidally down to 7.6 m or more (Eldridge and Kaill 1973). They appear to prefer substrates covered with seaweed, eelgrass, or rock upon which to deposit their adhesive eggs although the eggs commonly blanket every available surface during the height of spawning activity. Fecundity is 18,600 eggs for females averaging 192-mm standard length, and 29,500 eggs for females of 223 mm (Hart and Tester 1934). Most spawning occurs at night, although fish have been observed to spawn during the day as well, and at all tidal stages. The eggs range between 1.3 to 1.7 mm in diameter and are usually deposited one or two eggs thick, but can be in layers up to 51 mm deep (Miller and Schmidtke 1956). Eldridge and Kaill (1973) found that when heavy "clumping" of eggs occurs, survival is poor among all but the outlying eggs.

During and after spawning, adult fishes and eggs are subjected to heavy predation from the many sea birds, fishes and sea lions that gather at the spawning grounds. Mortality of eggs may range from less than 5% in deep water to 99% or more for intertidal spawning where eggs are available to a variety of predators, particularly gulls (Eldridge and Kaill 1973). After leaving the Bay, postspawning adults and juveniles are thought to disperse along the coast (J. Spratt pers. comm.) and a significant number apparently migrate to Monterey Bay where the commercial fishery regularly lands nonspawning herring.

History of the Fishery

Immigrant Italian fishermen started fishing for herring about 1850, and by 1888, 35 to 40 boats were engaged in the fishery which was centered in Richardson Bay (Skinner 1962). There was also limited fishing over the shallows on the eastern side of San Francisco Bay south of Alameda and off Point Richmond. Fishermen used gill nets, beach seines, and later paranzella nets. The bulk of the landings was sold in the fresh fish markets, but when abundant and cheap, part of the catch was salted and sold for bait as well as for human consumption. According to Collins (1892) herring landings in 1888 amounted to 1,200 t.

Attempts to establish export markets failed because Pacific herring did not measure up to the quality of Atlantic herring. Bay fish were particularly unsuitable because of their small size,

SMITH AND KATO: FISHERIES

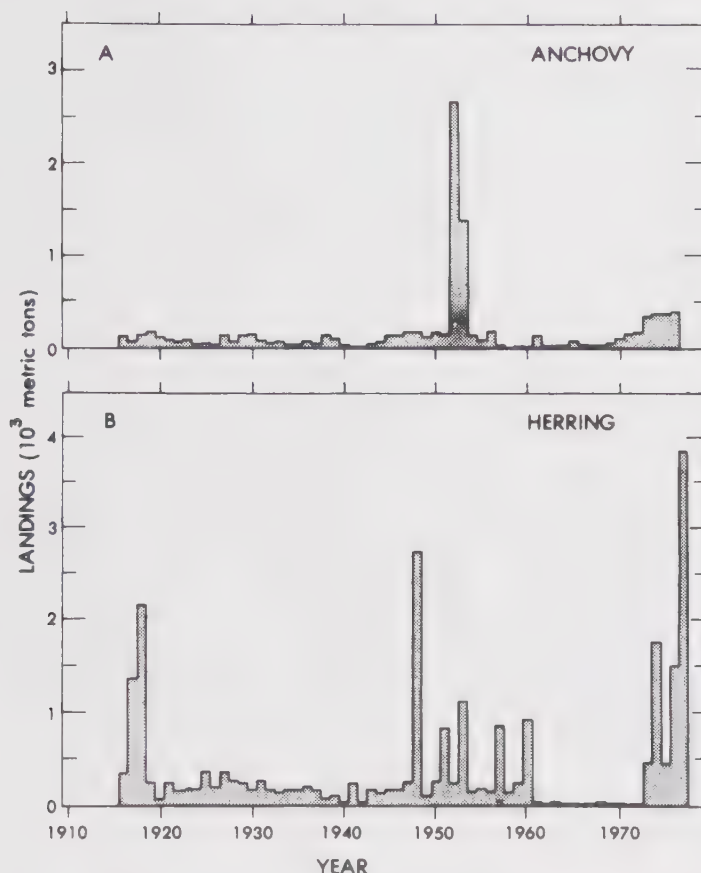


Fig. 4. Commercial fish catches in the Bay: (A) Anchovy (1916-1976); (B) Herring (1916-1976/77 season).

and because gill netters and seiners took only spawning fish that were not in prime condition for salting and smoking (Scofield 1918). Some salted herring was shipped to the Orient, however.

Demand for herring increased as food came into short supply during World War I. In 1917 a canning and reduction plant was established at Pittsburg, California, supplied by fish from San Francisco and Tomales bays, particularly the latter, because the fish were fatter and longer (Scofield 1918). Although the San Francisco Bay catch rose to nearly 2,150 t in 1918 (Fig. 4B), the fishery was short-lived. In 1921 the State Reduction Act was enacted, limiting reduction of fish to fish meal. Canning operations closed and from 1920 through 1946 only small quantities were landed for fresh consumption, bait, and for smoking (Frey 1971; Miller and Schmidtke 1956).

The fishery had a brief revival after the end of World War II when herring was tried as a substitute for the vanishing sardine, but the attempt was unsuccessful. Thereafter only a small pet-food market continued to provide a limited demand, but even this market did not hold (Eldridge and Kaill 1973).

In the mid-1960's, a specialized fishery began for herring eggs, utilized in Japan in two forms: "kazunoko" and "kazunoko-kombu." Kazunoko consists of the ovaries taken from ripe

SAN FRANCISCO BAY

herring. Fish are taken by lampara nets, gill nets, and purse seines. Kazunoko-kombu refers to herring eggs-on-kelp, which is gathered by divers in subtidal areas. Both products are expensive gourmet items in Japan.

As fishing effort intensified in both Tomales and San Francisco bays, public concern mounted over the fate of the herring resource, and emergency legislation was passed in 1973 that instituted a permit and quota system for the herring fishery. In San Francisco Bay, the present (1977-1978) quota for adult herring is 4,558 t; the quota for eggs-on-kelp is 4.5 t, including plant material. The commercial season extends from December 14 through March 31 with different starting dates for the various fishing methods.

The 1976-77 herring spawning population in San Francisco Bay was estimated at 24,489 t (J. Spratt pers. comm.).

NORTHERN ANCHOVY

Probably the most abundant species of fish in the Bay, the northern anchovy, *Engraulis mordax*, supports a modest commercial fishery and is important in the food web. The anchovy is a short-lived species, attaining a probable maximum of seven years, although rarely exceeding four years of age and a length of 18 cm (Frey 1971). Sexual maturity is reached by the end of two years at a length of about 13 cm (Frey 1971).

Anchovy are found in the Bay throughout the year, but a large influx occurs in May, and an elevated abundance persists through September (Aplin 1967). Commercial landings also coincide with this period, but high catches extend into October and sometimes into November (DFG Catch Bulletins). Many small anchovy can be found during this period, indicating that the species probably spawns in the Bay. Eldridge (1977) found the greatest number of larval anchovy during December, however.

Many species of fish feed on anchovy of appropriate size, including downstream migrant salmon (Heubach 1968), jacksmelt (Boothe 1967) and striped bass (Johnson and Calhoun 1952). Indeed, because of its abundance and small size the anchovy is probably the most important forage fish in the Bay.

The Fishery

From 1916 through 1951, annual landings of anchovy in the Bay Area (Fig. 4A) amounted to less than 180 t (Skinner 1962). In 1952 the catch increased suddenly to 2646 t due to the need for a substitute for the failing sardine industry. Because of low consumer acceptance of canned anchovies, and rigid state laws governing reduction of fish into fish meal, catches in subsequent years declined considerably. Recently, however, the landings have started to increase again, and the commercial catch has stabilized at around 385 t (M. Oliphant pers. comm.).

Practically the entire reported catch is now preserved and packed as frozen bait for recreational fisheries. An additional unrecorded amount, perhaps as much as 25% of the "dead bait" landings, is taken for use as live bait, primarily for use in the sport fishery for striped bass. In some years both live and dead anchovy are also used as bait in the commercial albacore tuna fishery. The landed value of the 1974 "dead bait" catch was \$73,344 (McAllister 1976).

Although anchovy for the bait industry are normally caught within the Bay, in some years about 10% are caught outside the Golden Gate (W. Millazzo, Meatball Bait Co., Sausalito; and W. Beckett, bait dealer, Oakland, pers. comms.). We have no estimates of the tonnage caught outside the Bay during the two years of greatest landings (1952 and 1953).

Anchovy are caught in the Bay exclusively with a roundhaul seine called a "lampara" net.

SMITH AND KATO: FISHERIES

When the anchovy are to be kept alive the fish are dip-netted from the seine into holding tanks aboard the fishing vessel. At times the entire net with the encircled school of anchovy is towed to a moored bait receiver.

No estimates are available on the abundance of anchovy in the Bay. Since the greatest bulk of anchovy are seasonal migrants, it seems unlikely that the stocks in the Bay can be imperiled by the present fishery.

STARRY FLOUNDER

The starry flounder (*Platichthys stellatus*) is one of the most important sport-caught flat-fishes along the Pacific Coast (Squire and Smith 1977). It is euryhaline, commonly occurring in estuarine areas, and sometimes in full fresh water and appears to prefer a soft sand habitat (Orcutt 1950). The main spawning period is December-January, when mature starry flounder apparently migrate to shallower waters (Orcutt 1950). Average size of individuals taken during a bottom trawl survey in San Francisco Bay was 41 cm, with a range of 24-63 cm (Boothe 1967). According to Orcutt (1950) a 41-cm fish weighs about 1.5 kg and would be sexually mature. Lockington (cited by Orcutt 1950) reported in 1880 that large starry flounder from 3.6 to 5.4 kg occurred in San Francisco Bay. Fish of this size are rarely encountered today.

Although mature starry flounder are common and some spawning would be expected to occur within the Bay, only few eggs, larvae, and juveniles have been taken in surveys (Green 1975; Eldridge 1977). Ganssle (1966) found that size of starry flounder decreased with distance upstream from San Francisco Bay. D. Stevens (pers. comm.) reports that few starry flounder are found in the Delta, but large ones are commonly caught in San Luis Reservoir, suggesting that the young are carried from the Delta to the Reservoir via the aqueduct. Food of starry flounder in San Francisco Bay consists primarily of polychaete worms, small bivalves, siphons of larger clams, and small crabs (Boothe 1967).

The Fishery

The starry flounder is an important species to anglers in the Bay as it is an excellent food fish. Bottom fishing from anchored or drifting boats in San Pablo and Suisun bays probably produces the best catches, although this species is also common in the shore catch. The commercial fishery for starry flounder is conducted almost exclusively by bottom trawl in offshore coastal waters; no commercial fishing occurs in San Francisco Bay. No data are available on the abundance of starry flounder in the Bay. Sampling with a bottom trawl disclosed its presence at all stations, from Palo Alto to Richmond, and although it ranked 16th in total numbers captured (Aplin 1967), its large size should relegate it to a higher position in terms of biomass.

SURFPERCH

About a dozen species of surfperch (family Embiotocidae) occur in San Francisco Bay, the most common being the pile (*Damalichthys vacca*), black (*Embiotoca jacksoni*), shiner (*Cymatogaster aggregata*), walleye (*Hyperprosopon argenteum*), white (*Phanerodon furcatus*), rubberlip (*Rhacochilus toxotes*), striped (*Embiotoca lateralis*) and rainbow (*Hypsurus caryi*) surfperches (Wooster 1968a; Squire and Smith 1977). Surfperch are relatively small coastal marine fishes, although the larger species, such as the pile and rubberlip, are known to reach lengths of 44 and 47 cm, respectively (Miller and Lea 1972).

All embiotocids are viviparous—a reproductive process rare among marine teleosts. Breeding habits have been described for some surfperch species (Eigenmann 1894; Wales 1929; Rechnitzer

and Limbaugh 1952; Engen 1968; Wares 1971; and others). In general, mating usually takes place shortly after a previous brood has been released and the sperm may be carried for months by the female before the eggs are fertilized. The embryos develop in membranous sacs and receive nourishment from the surrounding ovarian fluid. The young are well developed and independent at birth (Wares 1971; Frey 1971). It appears that many Bay surfperch release their young in spring and early summer, judging from the occurrence of term females in the sport catch at that time (W. Dahlstrom pers. comm.). To our knowledge, nothing has been published on movements and breeding habits of Bay surfperch, and in general, information on other life history aspects is lacking. Boothe (1967) found that shiner surfperch fed predominately on benthic invertebrates such as gammarid amphipods and cumaceans, and to a lesser extent on clams and polychaetes. Adams (unpublished)¹ found gammarid and caprellid amphipods were the most important food of black surfperch; other small crustaceans, tanaids and isopods were also important, as were polychaete worms and bryozoans. The diets of striped and rainbow surfperch were similar, but for pile perch, large crustaceans, hard-shelled molluscs and barnacles were much more important in the diet.

Because they occur and are caught in nearshore locations, often adjacent to highly populated and industrialized areas, surfperch and the organisms upon which they feed may be exposed to higher concentrations of pollutants than species inhabiting the deeper waters of the Bay where tidal action and outflow flushing aid in dispersal of these materials. Earnest and Benville (1971) found DDT levels to be higher in surfperch than in the flatfish, sculpin and crabs they sampled in the Bay.

The Fishery

Surfperch form an integral part of the marine sport catch in San Francisco Bay, and are frequently taken by pier and wharf anglers (Wooster 1968a; Squire and Smith 1977). Shiner perch is also a popular live bait for striped bass. Winter and spring are the best fishing times, when larger individuals are usually taken (Wooster 1968a).

Members of this family are of minor commercial importance locally, although some do occasionally appear in local markets. Before the turn of the century, however, surfperch were apparently quite common in San Francisco fresh fish markets (Eigenmann 1894, citing Lord). Judging from some of the early accounts (Wilcox 1898), most were taken with beach seines.

ELASMOBRANCHS (SHARKS AND RAYS)

Of the species of elasmobranchs occurring in San Francisco Bay, the most abundant is the brown smoothhound, *Mustelus henlei* (Herald and Ripley 1951; Russo and Herald 1968). The leopard shark (*Triakis semifasciata*), soupfin (*Galeorhinus zyopterus*), dogfish (*Squalus acanthias*), sevengill shark (*Notorhynchus maculatus*), and the bat stingray (*Myliobatis californica*) are all fairly common. The largest shark caught in the Bay was a rare sixgill shark (*Hexanchus griseus*) which measured about 3.3 m and weighed 210 kg (Herald and Ripley 1951). Total biomass of these species is unknown but may be considerable. One study using bottom longline gear produced a catch rate of 15 sharks per 100 hooks (Herald and Ripley 1951), which is an exceptionally high catch rate for any commercial longline fishery.

South Bay apparently harbors more sharks than the central and northern reaches (Herald and Ripley 1951). The brown smoothhound and leopard sharks apparently prefer shallower waters, while the sevengill is usually found in waters deeper than 6 m. The Bay may be a nursery ground for some sharks, as evidenced by the predominance of juveniles in the catch. Soupfin gives birth to pups in the Bay (Herald and Ripley 1951), and we have caught many pregnant brown smoothhounds with near-term pups.

¹ "Resource partitioning among members of a model fishery." NMFS, Tiburon Lab., Tiburon, CA 94920.

Food habits of leopard sharks and brown smoothhounds have been extensively studied by Russo (1975) who found that both were essentially benthic feeders. Disturbingly, he also found polychlorinated biphenyl (PCB) levels of 22-47 ppm in the liver, and total identifiable chlorinated hydrocarbon levels of 37 and 108 ppm respectively for smoothhound and leopard sharks. Among the important food elements (over 15% frequency of occurrence in stomachs of sharks caught in San Francisco Bay) were shrimps, crabs, herring eggs, and the fat innkeeper worm (Russo 1975).

The bottom-feeding mode of these two species apparently was connected to a case of mass mortality recorded in 1967 (Russo and Herald 1968). During a period of 33 days, more than 725 elasmobranchs were found dead along the banks of the eastern shore of San Francisco Bay. Of this total 492 were brown smoothhounds. Leopard sharks and bat stingrays, presumably a bottom feeder also, made up the rest of the total killed, except for a solitary sevengill shark. The cause of death was not determined.

History of the Fishery

Presently no commercial fishery exists in San Francisco Bay for elasmobranchs. During the celebrated "boom" of shark liver oil that lasted from 1937 through the early 1950's, an intensive fishery was conducted throughout the state for soupfin and spiny dogfish (Ripley 1946; Frey 1971). The livers of these species, particularly the soupfin, are rich in Vitamin A. During this period landings of sharks from the San Francisco Bay region constituted over 40% of the total for the state (Ripley 1946). Between 1937 and 1945, annual landings of all sharks in the San Francisco Bay area averaged 870 t, with a high of 2,243 t in 1940.

Ripley's (1946) figures indicate that during 1941-44, soupfin constituted 16% of the total shark landings in the San Francisco region. Presumably most of the remainder were spiny dogfish, much of which were caught by bottom trawl gear outside the Bay. Byers (1940) indicates that a large proportion of the soupfin landed in the San Francisco region were caught by hook and line within the Bay.

Shark and ray fishing is popular with many Bay anglers, and although most people disdain the thought of eating sharks, some species are considered desirable and are commonly eaten. In fact, all the species found in San Francisco Bay have been found in the market (Frey 1971). The leopard shark and soupfin are particularly desired for their substantial amounts of firm white flesh, and many anglers in San Francisco Bay undoubtedly consume these species regularly. A further use of shark, one heartily recommended by gourmets, is the Chinese sharkfin soup.

CLAMS, OYSTERS, AND MUSSELS

San Francisco Bay contains large numbers of shellfish species, some of which have known potential commercial and recreational value such as the soft-shell clam, Japanese littleneck, mussels, and the native oyster (see also Carlton 1979 and Nichols 1979). Although considerable progress has been made in improving water quality in the Bay in recent years, shoreline waters are apparently not yet free enough of sewage contamination for the State Public Health Department to sanction harvesting of Bay shellfish for consumption.

History of the Fisheries

San Francisco Bay was one of the major landing areas in the State for oysters and clams, but these fisheries declined steadily after 1900, with the oyster industry collapsing in the late 1930's, and the soft-shell clam industry in the late 1940's (Skinner 1962; Jones and Stokes 1977). By and large, introduced species have been the most important commercially.

Oysters: Three species of oysters were harvested from San Francisco Bay in the past: the native oyster (*Ostrea lurida*), the eastern oyster (*Crassostrea virginica*), and the Pacific or Japanese oyster (*C. gigas*). The latter two species are exotics introduced for holding and fattening or seed culture—neither have reproduced sufficiently in the Bay for commercial exploitation (Jones and Stokes 1977). Information on these oyster fisheries can be obtained from Bonnot (1935), Skinner (1962), and Wooster (1968c).

The native oyster was once extremely abundant in many parts of the Bay (Townsend 1893). This species was harvested centuries ago by local Indian populations and briefly for the restaurant trade during and after the Gold Rush days (Wooster 1968b; Jones and Stokes 1977). It could not compete with the larger, more desirable eastern oyster after the latter was introduced, however. Apparently no attempts have been made to culture the native oyster in the Bay, and although at least five large native oyster beds still exist (Wooster 1968b), the species is much less abundant than it was before the turn of the century. The decline in native oyster populations is thought to be the result of predation by the eastern oyster drill which was introduced with the first eastern oyster shipments from the Atlantic Coast, and the silting in of much of the suitable substrate that once existed (Bonnot 1938; Wooster 1968b).

Clams and Mussels: Three of the most abundant species of bivalves are not native to the Bay, and all were accidental introductions. These are the soft-shell clam (*Mya arenaria*); the ribbed or horse mussel (*Ischadium demissum*); and the Japanese littleneck (*Tapes japonica*). The bay mussel (*Mytilus edulis*) is considered indigenous to this coast; however, some populations may represent exotic stocks introduced by way of ship fouling (D. Chivers pers. comm.; Carlton 1979).

The soft-shell clam was introduced into California with shipments of eastern oysters in 1869 or 1870 and first detected in 1874 (Fitch 1953). It became abundant and widely distributed in the Bay in the late 1880's and soon formed the bulk of the clam trade in San Francisco (Wooster 1968b). Apparently *Mya arenaria* largely displaced native clams in the Bay, especially the bent-nose clam (*Macoma nasuta*) in the South Bay, where prior to 1876, large numbers were harvested by Chinese fishermen (Skinner 1962; Weymouth 1920). According to Wilcox (1895), from 1889 to 1892, between 500 and 900 t of soft-shell clams were taken in the Bay each year (Fig. 5A). In 1899 Bay landings amounted to 695 t valued at \$21,908 (Wilcox 1902).

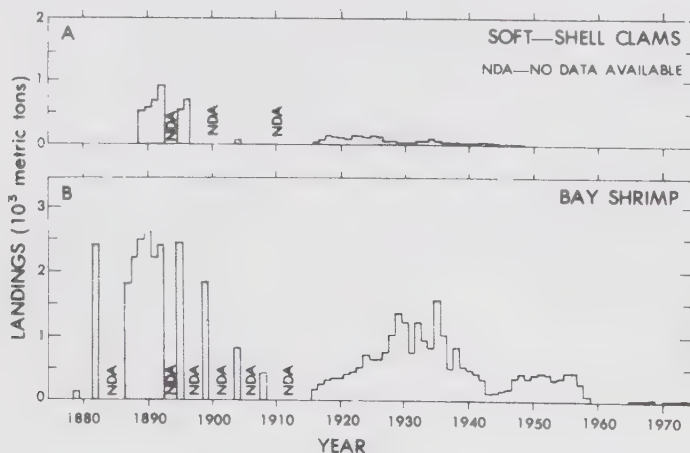


Fig. 5. Shell-fish commercial catches in San Francisco Bay: (A) Soft-shell clams (1889-1948); (B) Bay shrimp (1879-1974).

After the turn of the century, landings dropped considerably. In 1916 only 245 t were sold, and by 1927 the take had declined to 68 t (Wooster 1968b). By the early 1930's several beds had been destroyed or abandoned due to expiring leases and pollution (Bonnot 1932). The commercial fishery for soft-shell clams had disappeared by 1949. Its decline has been attributed to a variety of factors; domestic and industrial waste pollution, bay filling and construction; overharvesting; the high cost of manual labor required to dig the clams; and State allocation of some of the better clam beds for recreational use only (Bonnot 1932; Skinner 1962; Wooster 1968b).

During the time the soft-shell clam industry was collapsing, another exotic food clam, the Japanese littleneck (*Tapes japonica*) was becoming established. It was apparently introduced with shipments of Pacific oyster seed during the early 1930's, and since that time it appears to have taken over much of the habitat formerly occupied by the native littleneck or rock cockle, *Protothaca stamina* (Jones and Stokes 1977; Ricketts and Calvin 1968).

Soft-shell clam and Japanese littleneck are presently abundant in the Bay, and although subjected to intensive sport clamming in such areas as Foster City and Berkeley (despite warnings of the Public Health Department), these resources remain essentially unused (Jones and Stokes 1977; W. Dahlstrom pers. comm.).

The soft-shell clam prefers sheltered bays and a heavy mud substrate where there is some mixing of fresh and salt water (Fitch 1953). Heavy wave action is detrimental to the species (Matthiessen 1960). Recently over 1 million clams were destroyed in the Corte Madera-San Quentin area, possibly the result of wave scouring caused by the new Larkspur commuter ferry (R. McAllister pers. comm.).

The Japanese littleneck apparently can survive within a wide salinity range. It adapts well to extreme saline conditions and has also been found in the estuary where salinities were as low as 16 ‰ (Wooster 1968b). The species appears to prefer gravel bottom, and does not develop on substrates where no attachment is possible or where the young may be subjected to gill clogging (Filice 1958; Wooster 1968b).

The bay mussel, *Mytilus edulis*, like the soft-shell clam, contributed substantially to the Bay shellfish harvest in times past, especially prior to 1895. Between 1889 and 1892, San Francisco Bay mussel landings fluctuated between 950 and 1300 t per year (Wilcox 1895). Soon afterward the fishery suffered a severe decline which was attributed to reports of people becoming ill from eating bay mussels. At the present time it is utilized mostly for bait and occasionally for food. Although considered a delicacy in Europe where it is cultured commercially, it is not much sought after locally (Fitch 1953).

The ribbed mussel, *Ischadium demissum*, is another abundant mytilid in the Bay. It was apparently introduced with oyster shipments in the 1870's, and though it has occurred in San Francisco markets in the past, it has never been an important food item (Jones and Stokes 1977). Because of its high Vitamin D content, a proposal was made in the early 1960's to harvest *I. demissum* for use in freeze-dried form as a food additive, but the venture fell through because of Public Health restrictions (Aplin 1967; Jones and Stokes 1977).

The ribbed mussel lives in the high intertidal zone, most often in association with the native cord grass (*Spartina foliosa*), and the species is capable of filtering out great quantities of suspended matter from the water (Aplin 1967). The continual sedimentation effected by mussels may play a large part in salt-marsh development and mussel populations may also be important in the estuarine phosphate cycle by furnishing raw materials to deposit feeders which in turn regenerate the phosphate (Kuenzler 1961).

Paralytic shellfish poisoning (PSP) is commonly associated with mussels and results from the consumption of shellfish that have been feeding on toxin-producing dinoflagellates of the genus *Gonyaulax* (Ricketts and Calvin 1968). Most, if not all, cases of PSP in California are probably

associated with the sea mussel, *Mytilus californianus*, not the ribbed or bay mussels; however, all mussels are under State quarantine from May through October, when blooms of *Gonyaulax* are known to occur (Jones and Stokes 1977).

Public Health Problems and the Future

The combination of rapid population growth and industrialization since 1900 has undeniably affected shellfish resources in San Francisco Bay. Skinner (1962) points out that even before the turn of the century, pollution, siltation and ship wastes were hastening the decline of the fisheries in the Bay, and that shellfish were particularly vulnerable. He cites an 1878-79 Board of Fish Commissioners report by W. N. Lockington, who attributed the decline not just to overfishing and increased boat traffic, but in particular, to the "constant fouling of the waters and destruction of life by the foetid inpourings of our sewers . . ."

In 1932, bacterial levels in the Bay were so high that the State Board of Health passed a resolution establishing a general permanent quarantine on shellfishing in San Francisco Bay, but this quarantine was rescinded in 1953 (Jones and Stokes 1977).

No comprehensive sanitary survey has been conducted in the Bay although bacterial surveys are made at irregular intervals at various locations by certain governmental agencies. These surveys have revealed a significant improvement in water quality over the past 10 years (California Water Quality Control Board 1976); however, Jones and Stokes (1977) point out that results obtained during the past two drought years may be misleading due to the reduction of urban runoff, a significant contributor to high bacterial levels. Even if bacterial quality reaches acceptable levels, other problems still need to be resolved such as uncontrolled urban run-off during storms, presence of harmful viruses, uptake and concentration of harmful trace metals and other toxic substances; and sport-commercial allocation of the resource.

BAY SHRIMP

Three species of native shrimp occur in San Francisco Bay: *Crangon franciscorum*, *C. nigricauda*, and *C. nigromaculata*. The Korean shrimp, *Palaemon macrodactylus*, which was introduced accidentally in the early 1950's, has also become established in brackish waters of the Bay system (Ricketts and Calvin 1968). Of the crangonids, the largest and most abundant is *C. franciscorum*, followed by *C. nigricauda*. *C. nigromaculata* is far less numerous and is not considered in this chapter.

Bay shrimp are important forage for sport and market fishes. In the Bay they occur frequently in the diet of sturgeon (McKechnie and Fenner 1971) and striped bass (Johnson and Calhoun 1952). Moulting by bay shrimp and agitation of bottom sediments in their search for food and protection may also contribute to the cycling of nutrients (Krygier and Horton 1975).

Much of the life histories of *C. franciscorum* and *C. nigricauda* are similar (Israel 1936). Both species breed at the end of their first year. Females attain a larger size than males, and at maturity measure approximately 37 mm TL (*C. nigricauda*) and 53 mm TL (*C. franciscorum*). The eggs hatch in water of high salinity. Larval stages are planktonic until reaching 6 to 7 mm in length, at which time they settle to the bottom and move toward shallow water of reduced salinity. The earliest postlarval shrimp are found in brackish or nearly fresh waters of tidal flats or sloughs. As the shrimp develop and spawning season approaches, they move back into deeper, cooler, and more saline water.

Ovigerous females occur throughout the year, but Israel (1936) found that major spawning occurred from December to May or June for *C. franciscorum* and from April to September for *C.*

nigricauda. Krieger and Horton (1975), however, found a bimodal spawning pattern for the same species in Yaquina Bay, Oregon. Ganssle (1966) observed ovigerous *P. macrodactylus* in Suisun Bay during fall sampling.

Of the crangonids, *C. franciscorum* is the more tolerant of fresh water and has been found far up into the Delta, while the upper limit of *C. nigricauda* is in Suisun Bay, and then only in the fall with intrusion of salt water (Skinner 1962). This difference may be an important factor separating the two species and limiting competition, although it is possible that this balance may have been disrupted in some way with the introduction of the Korean shrimp.

Little data are available on the population size and species distribution in the Bay, although the present bait fishery appears to be far from utilizing the full potential of the resource (Frey 1971). Because bay shrimp are short-lived there may be large fluctuations in abundance from year to year, and, for the same reason, shrimp populations would be particularly sensitive to the effects of short-term pollution in the environment (Frey 1971).

History of the Fishery

Scofield (1919), Israel (1936), and Skinner (1962) have provided summaries of the development of the bay shrimp fishery. According to these authors, shrimp fishing in California was started in 1869 by Italian fishermen who employed 18 m long seines and sold their limited catch to local fish markets. The Chinese entered the fishery in 1871 with the far more efficient Chinese shrimp net or "bag net," which greatly increased the catch and promptly put the Italian fishermen out of business. The Chinese nets were funnel-shaped stationary traps, 9 m across, 12 m long and operated by tidal action. The local demand for shrimp was not great, but a profitable export trade was built up from the dried product which was shipped to the Orient. An estimated 1,500 Chinese were engaged in the fishery in 1875. Between 1882 and 1892, yearly catches averaged 2,270 t (Fig. 5B). In 1897, 26 Chinese shrimp camps were established at various locations around San Francisco Bay. This number was reduced to 19 camps by 1910.

The use of Chinese shrimp nets met with opposition from the beginning, because many juvenile food fishes were allegedly destroyed incidental to the shrimp catch, and later because it appeared that the shrimp resource was being rapidly depleted. Thus a series of laws was passed from 1910 to 1919 involving closed seasons, gear restrictions and processing limitations. After 1915 Chinese nets were allowed only in South Bay, while beam trawls were used elsewhere.

In following years the number of shrimp camps diminished, but the catch rose steadily until 1929, then fluctuated around 1000 t between 1930 and 1936, after which landings decreased steadily due to lack of a market for dried shrimp (Frey 1971).

In 1965 the fishery was revived to supply bait for striped bass and sturgeon sportfishing. Today there are about 15 boats in the fishery, and all but a few fish with beam trawls. Most fishing takes place in San Pablo and Suisun bays, and to a limited extent in South Bay. Although the size of the fishery is small, the business can be lucrative, as bait shrimp brings a price of \$2.00 to \$2.50 per pound (0.45 kg) to the fisherman. It is sold both frozen and live, the latter being in the most demand and bringing the highest price. The small size of bay shrimp appears to be the major factor limiting the demand for them as food, and at this time it does not appear that they can be processed economically for sale on a large scale.

DISCUSSION

The foregoing account illustrates the changing fortunes of the fishery resources of San Francisco Bay. The commercial landings, affected by regulations and environmental changes as

well as market demand and resource availability, have undergone drastic changes not only in quantity but also in the kinds of fishery resources harvested from the Bay. Formerly, bivalves, shrimp, salmon, and sturgeon, as well as a number of other finfishes, provided a substantial income to Bay Area fishermen. Now the only remaining commercial fisheries of note within the Bay are those for herring, anchovy and bay shrimp, and the latter two are used almost exclusively as bait.

Recreational fisheries, alternatively, have fared somewhat better, due primarily to legislation which has restricted commercial fishing for certain species and outlawed some fishing gear detrimental to stocks of incidentally caught fishes. Striped bass and sturgeon are now reserved exclusively for the sport fishery, as is chinook salmon fishing within the Bay.

Human activity is clearly implicated in the decline of much of the fishery resources of San Francisco Bay. Although the full effects of dumping, dredging and filling are not clear, we can safely surmise that filling of shallow mud flats around the perimeter of the Bay has drastically reduced the amount of suitable habitat for such forms as oyster, clams, and bay shrimp. Pollution has degraded the purity of water to the extent that even now after considerable effort to improve water quality, commercial and recreational use of molluscs is still hazardous and by and large discouraged or disallowed. In past years intensive harvesting also contributed to the decline of many Bay fisheries.

Anadromous fishes have suffered from the damming and diversion of rivers which resulted in elimination or alteration of spawning and nursery habitats. Changes in the hydrography of the Delta caused by diversions, and pollution from industrial, agricultural, and municipal waste discharges may not only affect these fishes directly but may also affect the distribution and abundance of forage species upon which they depend.

Research Needs

A review of the literature discloses that except for bivalves and a few finfish (striped bass, herring, sturgeon, salmon) little quantitative data are available on the fishery resources of San Francisco Bay. Neither is there much information on the life history of most of the animals which reside in the Bay, whether they be seasonal migrants or residents. There is also a need to study trophic relationships and interspecific interactions in order to better gauge the effects of changes in the environment.

The Future

It is likely that reduction in duration and frequency of fresh-water flows into and out of the Delta, caused by increasing demands for water for agricultural, industrial and domestic use, will further affect anadromous fish stocks unless steps are taken to prevent or replace losses caused by reduced flows. The gradual decline in the amount of fresh-water flow out of the Delta will probably alter salinity regimes in the Bay, which may change the distribution of certain species and possibly the migratory habits of anadromous fishes and invertebrates such as the salinity-regulated crangonids.

The full effects of the recent drought (1976-77) on anadromous fishes is not known, and may not be felt for years to come when the fish spawned during the past few years begin to enter the fisheries. There may be a severe decline in the population resulting from poor spawning and year-class survival.

On the positive side, if water quality continues to improve in San Francisco Bay proper as it has over the past 10 years, we may see increased shellfishing in the Bay and perhaps the opening up of certain clamming areas that are now considered restricted by the California Department of Public Health.

SMITH AND KATO: FISHERIES

Prediction of what will happen in the future is difficult if not impossible, not only because of the complexity of the estuary itself and lack of knowledge of environmental requirements of many Bay species, but also because the San Francisco Bay estuary is obviously no longer a natural system. Factors such as water quality, water flow and habitat conditions are now largely under human control. Resource-related decisions made now and in the future will ultimately determine the fate of the Bay's fisheries. The value of these resources, perhaps now more than ever, will have to be weighed carefully against land and water use demands.

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ANALYSIS OF A SIMPLE MODEL FOR ESTIMATING HISTORICAL POPULATION SIZES

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ABSTRACT

Estimates of historical abundance of animal populations are important in many management decisions. Historical estimates based on a simple model of population growth have been made for several populations of dolphin involved with the yellowfin tuna purse seine fishery. We used the data for the bridled dolphin, *Stenella attenuata*, to investigate the behavior of the model by which these historical estimates were calculated. For populations with low net reproductive rates, the effect of bias in the estimates of the input parameters on the estimated historical abundances was approximately linear and additive. When all the input parameters were independently estimated, the variances of the historical abundance estimates were dominated by the variance of the initial abundance estimate and the coefficient of variation of the historical estimate was less than the largest coefficient of variation of any parameter.

Many decisions about the management of animal populations are based on the estimates of abundance of the population relative to its historical or preexploitation size. These estimates are basic to any application of the theory of maximum sustained yield as incorporated in several international marine mammal management agreements such as the North Pacific Fur Seal Treaty and the International Whaling Convention. Similarly, the concept of "optimum sustainable populations" as specified in the recent Marine Mammal Protection Act of 1972 (MMPA) has been defined in terms of comparing the present size of a population with its original size (Southwest Fisheries Center³). Schools of dolphin of several species (primarily *Stenella attenuata* and *S. longirostris*) have been used by purse seine fishermen in the eastern tropical Pacific to locate yellowfin tuna, *Thunnus albacares*, since 1959, as described by Perrin (1969). Significant numbers of dolphin have been killed by becoming entangled in the purse seines. In order to make management decisions under the MMPA about these dolphin populations, the National Marine Fisheries Service (NMFS) needed

estimates of the preexploitation abundance of the various populations. The NMFS convened a workshop of scientists to obtain the estimates based on a simple model of population change (see footnote 3). This paper evaluates the behavior of estimates of abundance obtained from their approach. This is important in order to be able to evaluate the degree of confidence to be placed in such estimates, and hence in management plans based on them.

METHODS AND MATERIALS

The model used to estimate preexploitation abundance is based on a common discrete model of population growth:

$$N_{\tau+1} = N_{\tau} - K_{\tau} + (N_{\tau} - K_{\tau})(b - d) \quad (1)$$

where N_{τ} = the abundance at time τ

b = the birth rate

d = the natural death rate

K_{τ} = the number of animals killed, assumed to occur at the beginning of time interval τ

$N_{\tau+1}$ = the abundance 1 time unit later.

Reversing the procedure (i.e., solving the above equation for N_{τ}) results in the expression

$$N_{\tau} = \frac{N_{\tau+1}}{1 + R_{\tau}} + K_{\tau} \quad (2)$$

where N_{τ} now is the estimate of abundance 1 yr

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³Southwest Fisheries Center. 1976. Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Pacific Yellowfin Tuna Fishery. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep. LJ-76-29, 53 p.

earlier and R_τ is the net reproductive rate ($b-d$). The above model was modified in the procedure used by NMFS to account for situations when the kills occur throughout the time interval instead of instantaneously at the end of the interval, as:

$$N_\tau = \frac{N_{\tau+1} + 0.5K_\tau}{1+R_\tau} + 0.5K_\tau. \quad (3)$$

This equation can be repeatedly applied to give estimates any number of years (t) into the past. When rearranged to explicitly display the population size t years earlier, and relabeling so that the initial abundance is N_0 , one obtains

$$N_t = \frac{N_0}{\prod_{j=1}^t (1+R_j)} + \sum_{j=1}^t \frac{K_j(1+R_j/2)}{\prod_{i=j}^t (1+R_i)}. \quad (4)$$

Note in this form that the time-index t runs backwards from zero. As is apparent in this form, the estimation of abundance t years earlier involves $2t+1$ parameters. The sequences of annual kills and net reproductive rates can be termed the kill and the net reproductive rate vectors, each composed of t elements.

The data used here to explore this estimation procedure is from the report of NMFS Workshop discussed above (see footnote 3).⁴ From existing unpublished data and reports the Workshop participants used estimates of the population size in

⁴It should be noted that the estimates used here are based on a number of assumptions currently under investigation and that these estimates are subject to significant change in the near future (I. Barret, Director, Southwest Fisheries Center, La Jolla, CA 92038, pers. commun. April 1978).

TABLE 1.—Estimates used for kill and reproductive rate vectors of *Stenella attenuata* in the eastern Pacific.

t	Year	Kill (thousands)	Net reproductive rate
1	1973	120	0.040
2	1972	273	.040
3	1971	185	.040
4	1970	308	.036
5	1969	331	.032
6	1968	164	.028
7	1967	194	.024
8	1966	281	.020
9	1965	297	.016
10	1964	255	.012
11	1963	133	.008
12	1962	106	.004
13	1961	446	.000
14	1960	534	.000
15	1959	129	.000

1974 and the annual incidental kills and reproductive rates from 1959 to 1974. Several sequences of estimated annual kills and reproductive rates were considered, incorporating the uncertainty in the data.

In the present paper the sequences of annual kills and net reproductive rates given in Table 1 are used to illustrate several general aspects of the behavior of Equation (4). These correspond to the "high kill" and "central reproductive rate" sequences for the bridled dolphin, *Stenella attenuata*, in the Workshop report. The estimate of 1974 abundance used by us and the Workshop was 3.5 million.

Estimation of Bias

A sensitivity analysis was done to examine the effects of biased parameter estimates on the backcalculated abundance. A new population size 1 yr earlier, from Equation (3), when each parameter is changed by a specified amount is

$$N'_1(n, k, r) = \frac{N_0(1+n) + 0.5K_1(1+k)}{1+R_1(1+r)} + 0.5K_1(1+k) \quad (5)$$

and in general for t years earlier,

$$N'_t(n, k, r) = \frac{N_0(1+n)}{\prod_{j=1}^t (1+R_j(1+r))} + \sum_{j=1}^t \frac{K_j(1+k) (1+(R_j(1+r)/2))}{\prod_{i=j}^t (1+R_i(1+r))} \quad (6)$$

where N_0 , R_i , and K_i are defined as above, and
 n = the proportion that N_0 deviates from its estimate
 r = the proportion that all elements of the net reproductive vector deviate from their estimates
 k = the proportion that all elements of the kill vector deviate from their estimates.

$N'_t(n, k, r)$ was then compared with N_t from Equation (4) or equivalently $N'_t(0, 0, 0)$. As a measure of the sensitivity of the basic model, $S_t(n, k, r)$ is defined to equal the percent that $N'_t(n, k, r)$ deviates from N_t .

$$S_t(n, k, r) = \left(\frac{N_t(n, k, r) - N_t}{N_t} \right) \cdot 100. \quad (7)$$

Estimation of Variance

The variance of the backcalculated estimate of N_t from Equation (4) was approximated using the delta method (Seber 1973). This method is based upon a Taylor series expansion for a function in which quadratic and other higher order terms are ignored. If f is a function of the random variables $x_1, x_2, x_3, \dots, x_n$ then the expression for the variance of f by the delta method is

$$V(f(X_1, X_2, X_3, \dots, X_n)) = \sum_{i=1}^n V(X_i) \left(\frac{\partial f}{\partial X_i} \right)^2 + 2 \sum_{i < j} \text{Cov}(X_i, X_j) \left(\frac{\partial f}{\partial X_i} \cdot \frac{\partial f}{\partial X_j} \right). \quad (8)$$

In applying this expression to Equation (4), it is necessary to be able to define which of the parameters should be considered as random variables, and to give reasonable estimates for value of the variances and covariances of these variables. For the purpose of exploring the behavior of Equation (4), we assumed that the estimates of all the parameters in Equation (4) are independent random variables. The covariance terms in Equation (8) are then zero. This approach provides a picture of the variance of the back estimate of abundance if in fact independent estimates of the kills and the net reproductive rates were available for each year. A generalized expression for the variance using this approach is

$$V(N_t) = V(N_0) \left(\frac{\partial N_t}{\partial N_0} \right)^2 + \sum_{j=1}^t V(K_j) \left(\frac{\partial N_t}{\partial N_j} \right)^2 + \sum_{j=1}^t V(R_j) \left(\frac{\partial N_t}{\partial R_j} \right)^2 \quad (9)$$

where all parameters are defined as for the basic model [Equation (4)]. For detailed expressions for each of the right hand terms see Appendix I.

As noted the method used for approximating the variance of a function depends on the higher order terms in the Taylor's series expansion being small. The higher order terms in the delta method expression for the variance of N_t are composed of the

second and higher order derivatives of N_t with respect to N_0 , K_t , and R_t , and the higher order central moments of the probability distributions of the estimates of N_0 , K_t , and R_t (i.e., skewness, kurtosis, etc.). The second and higher derivatives with respect to N_t and K_t are zero. Thus the terms involving R_t are the only higher order terms not equal to zero. The higher order derivatives of N_t with respect to R_t involve R_{t+1} to increasing negative powers. The three higher order moments of R_t are always decreasing since R_t is much less than one. Thus each of the higher order terms in the delta method expression for the variance of N_t are each less than the first order term in R_t (iii of Appendix I). The contribution of this first order term in R_t to the variance of N_t is small, as shown below. Thus the error induced by ignoring the higher order terms in the Taylor's series appears small.

The objective in doing the variance calculations was to understand the behavior of the variance of the population size when estimated by the basic back projection model [Equation (4)]. Thus a range of variances was calculated for a range of reasonable values of the variances of the estimated parameters. However, in our example of bridled dolphin estimates of the variance of many of the parameters were not available. Many of the kill estimates were not independently estimated and hence have large unknown covariances (Smith and Polacheck⁵). Estimates of net reproductive rate were obtained by extrapolation from other populations and from assumptions about density dependence. It is not clear that the uncertainty in these estimates can adequately be described by the notion of variance. Thus, the variances that we used and that we calculated for N_t should not be interpreted as actual estimates of variance for this population.

RESULTS

Bias

The results of the sensitivity analysis of the basic model will be presented by examining the effects of varying each of the variables n , k , and r of Equation (7), separately, and then in combinations.

The sensitivity of the back projected estimates

⁵Smith, T. D., and T. Polacheck. 1977. Uncertainty in estimating historical abundance of porpoise populations. Contract Rep. MM 7A C006, 39 p. Marine Mammal Commission, 1625 Eye Street, Washington, DC 20006.

(S_t) for a fixed number of years t into the past is linear with respect to n or k (Figure 1). This linearity can be seen in Equation (6) since n and k enter only as linear terms in the numerator. Positive

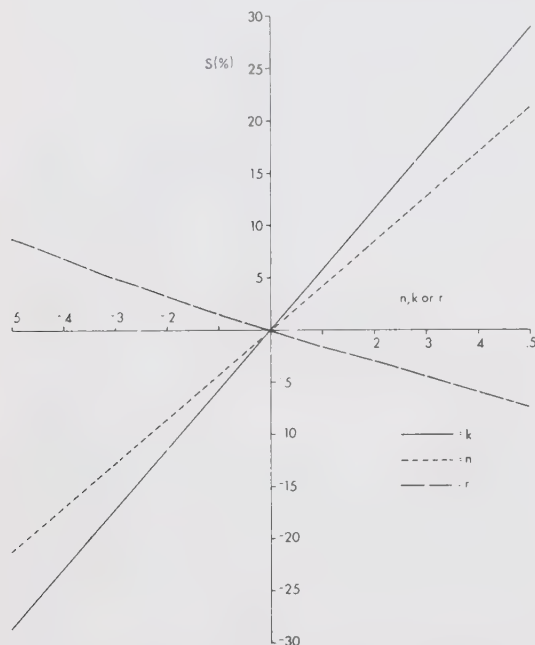


FIGURE 1.—Sensitivity of the model $S_t(n, k, r)$ in 1959 for a range of deviations in the initial number (n), for a range of deviations in the kills (k), or for a range of deviations in the net reproductive rate (r), for *Stenella attenuata* in the eastern tropical Pacific.

values of either n or k yield positive deviations in the back estimates. However, the farther back the population is projected in time, the smaller the contribution of N_0 to the back estimate becomes relative to the contribution of the kills. Thus the effect of bias in the estimate of the initial numbers (n) becomes progressively smaller the farther back in time the population is projected, while the consequence of a consistent bias in the kill estimates (k) becomes larger (Figure 2). Since the annual kills have no simple relationship to time, the effect of a particular value of n or k over time (Figure 2) cannot be described by any simple function. This trade off in the sensitivity of the back projected estimates between n and k is exact in the sense that for any decrease over time in the slope of S with respect to n there is an equivalent increase in the slope of S with respect to k . This can be seen by evaluating the partial derivatives of S with respect to n and with respect to k and noting that they sum to 1.

The effects of bias in the estimates of the net reproductive rate vector are more complicated than for the other two factors. Positive deviations in the net reproductive rates (r) yield negative deviations in the back projected estimate (Figure 2). The effect of r tends to increase over time (Figure 2). S approaches being linear with respect to r for any particular year, but unlike the relationship for k and n , this result is not exact (Figure 1). The approximate linearity of the sensitivity of N_t

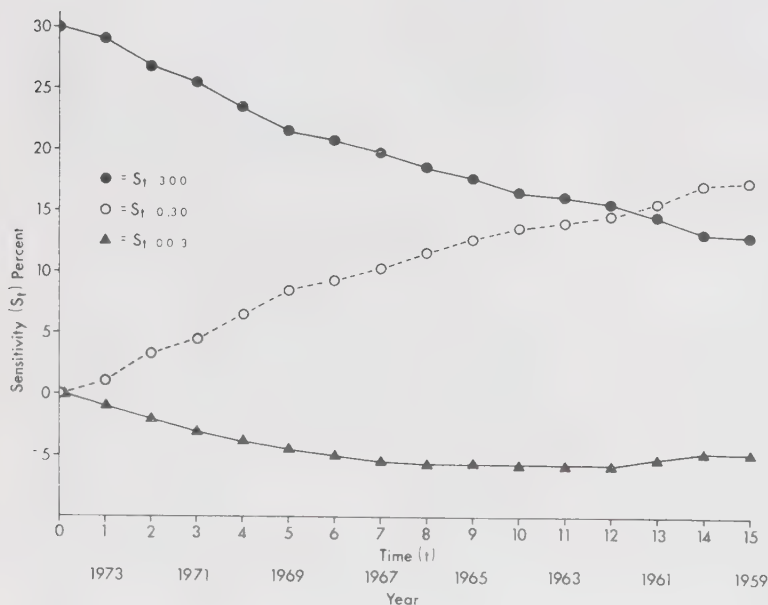


FIGURE 2.—Sensitivity of the model $S_t(n, k, r)$ over time to a 30% deviation in the initial number ($n = 0.3$), in the kill vector ($k = 0.3$), and in the net reproductive rate vector ($r = 0.3$) when all factors are held constant for *Stenella attenuata* in the eastern tropical Pacific.

to r appears to be a general feature of this procedure when r is small. This can be seen by examining S_t expressed as a function of r , which can be obtained explicitly by substituting the definitions of N_t [Equation (4)] and N'_t [Equation (6)] into Equation (7) and simplifying.

The consequences of having two factors varying simultaneously are shown in the series of contours of equal values of S from Equation (7) (Figures 3-5). These contour plots present a visual picture of the sensitivity of the back projection to the different factors. From this set of contour maps, it can be seen that the surface generated by S [Equation (7)] tends to be nearly linear. Since S has no nonlinear terms with respect to n and k , the surface described by S in these two dimensions is simply a plane (Figure 4). There are nonlinear effects between the net reproductive rate and both initial abundance and the sequence of kills. For the example examined here, the nonlinearity between k and r is insignificant. For instance, if r and k both equal 0.50, S deviates from a linear model by <1%. In general the nonlinearity between k and r will be insignificant as long as the kills in any one year do not represent a large proportion of the population and as long as r is relatively small. Also, for the data considered here, the nonlinearity between the net reproductive rates and initial abundance is small but not insignificant. For example, if both n and r equal 0.50, S deviates

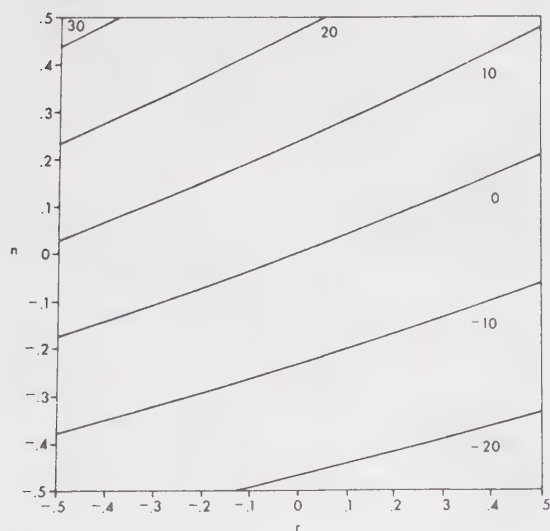


FIGURE 3.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the initial number (n) and in the net reproductive rate (r) when the kill vector is held constant for *Stenella attenuata* in the eastern tropical Pacific.

from a linear model by as much as 5%. This interaction effect is negative, resulting in a surface's bending downward from a strictly linear model when n and r have the same sign.

If all three factors vary together, the surface

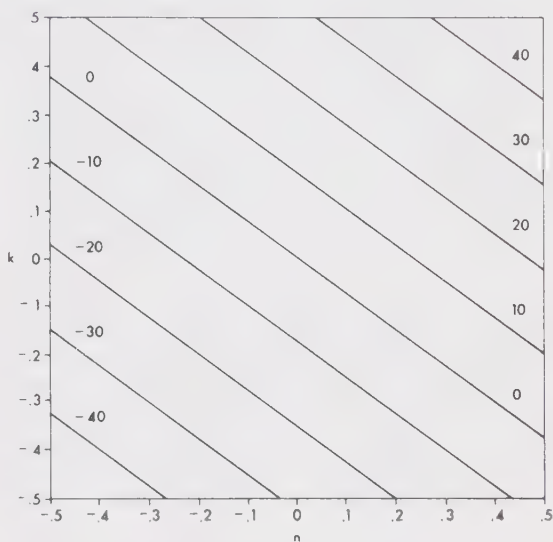


FIGURE 4.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the initial number (n) and in the kill vector (k) when the net reproductive rate vector is held constant for *Stenella attenuata* in the eastern tropical Pacific.

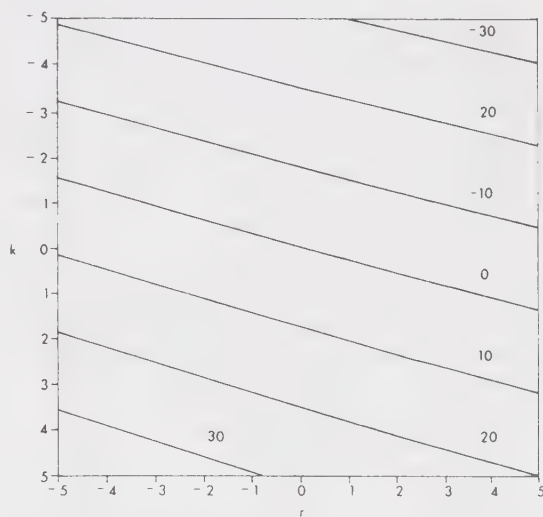


FIGURE 5.—Contours of equal sensitivity of the back estimated abundance in 1959 for a range of deviations in the kill vector (k) and the net reproductive rate vector (r) when the initial number is held constant for *Stenella attenuata* in the eastern tropical Pacific.

generated by S is still relatively linear as there are no terms in S containing n , k , and r and the pairwise nonlinear effects are small as discussed above. Table 2 provides examples of points on this three dimensional surface when n , k , and r are equal in absolute values. It can be seen there, for the example examined, that if the absolute values of n , k , and r are 0.10, the sensitivity of N_{15} ranges from -12 to $+12$.

An empirical equation can be fitted to the sensitivity surface (S) by fitting a linear function for each factor considered independently and by determining a nonlinear term for n and r . The general form of this fitted equation is

$$\hat{S}_t(n, k, r) = (b_1 K + b_2 n + b_3 r + b_4 nr) \times 100 \quad (10)$$

where the b 's are constant. The exact value of the b 's depends on the number of years the population is projected back in time. For the example considered here, projecting back from 1974 to 1959, the values of the b 's are shown in Equation (11):

$$\hat{S}_{15}(n, k, r) = (0.573k + 0.427n - 0.164r - 0.125nr) \times 100. \quad (11)$$

This empirical approximation [Equation (11)] deviates by <2 from the true values of S_{15} for values of n , k , and $r < 0.5$. This empirical equation is useful as the magnitude of the b 's provides a measure of the relative sensitivity of the different factors. Thus in Equation (11) it can be seen that for the example considered here the 1959 abundance estimate (N_{15}) is most sensitive to bias in the estimates of the kills. This empirical equation also provides an easy way to generate approximate values of S for any combination of values for n , k , and r .

Variance

The results of the variance calculations for the

TABLE 2.—Values of $S_{15}(n, k, r)$ when the absolute values of n , k , and r are equal.

Absolute value k = n = r	Sign of k	Sign of n			
		+		-	
		Sign of r +	Sign of r -	Sign of r +	Sign of r -
0.10	+	9	12	0	3
	-	-3	0	-12	-9
0.20	+	16	23	0	5
	-	16	1	-22	-17
0.30	+	24	36	1	8
	-	-10	2	-33	-26

bridled dolphin are summarized in Tables 3 through 6. Calculated values of the variance of N_t from Equation (9), when all of the random variables are assigned a coefficient of variation of 30%, are given in Table 3, over all years from 1974 to 1959. It can be seen that both the variances and the coefficients of variation (CV) generally decrease. The reduction of the CV over time is due to the fact that the major contributions to the back estimates of the population size are the addition of the kills of the previous years, since the reproductive rate is small. The variance of a sum of independent random variables is the sum of their variances. This always results in a CV for the sum which is smaller than the greatest CV of any of the random variables when the expected values of the random variables are positive (Appendix II). As a generalization, it can be stated that when the net reproductive rate is small the CV of the back estimate will not be larger than the largest CV of any of the random variables, and will usually be smaller.

Table 4 shows the breakdown of the variances calculated in Table 3 into their major components. The variance of N_0 is the major factor in the variance of these back estimates. The contribution of

TABLE 3.—Calculated variance and coefficient of variation for the back estimate of dolphin abundance when all random variables have a CV of 30%.

Year	Variance ($\times 10^{11}$)	CV (%)	Year	Variance ($\times 10^{11}$)	CV (%)
1974	11.03	30.0	1966	7.04	19.1
1973	10.22	29.0	1965	6.9	18.0
1972	9.53	27.0	1964	6.8	17.1
1971	8.88	25.7	1963	6.71	16.7
1970	8.35	23.8	1962	6.67	16.3
1969	7.99	22.1	1961	6.71	15.7
1968	7.56	21.2	1960	6.75	15.2
1967	7.25	20.2	1959	6.75	15.1

TABLE 4.—Breakdown of the variance of N_t into the major components that contribute to the calculated variance.

Year	Contribution to the variance of N_t ($\times 10^{10}$) due to the variance in:		
	The initial number	The kills	The net reproductive rate
1974	110.3	0.00	0.000
1973	101.9	.12	.156
1972	94.2	.76	.305
1971	87.1	.10	.452
1970	81.2	1.755	.568
1969	76.2	2.604	.664
1968	72.1	2.70	.735
1967	68.8	2.91	.784
1966	66.1	3.49	.816
1965	64.1	4.16	.835
1964	62.5	4.64	.843
1963	61.5	4.73	.843
1962	61.1	4.99	.840
1961	61.1	5.24	.840
1960	61.1	5.55	.840
1959	61.1	5.56	.840

TABLE 5.—Coefficients of variation (CV) for the back estimates of bridled dolphin in 1959 (N_{15}) for a range of CV for the parameters of the model. The ranges of CV's of the kills, net reproductive rate, and initial abundances were selected to illustrate particular aspects of the behavior of the variances of the back estimates.

CV of the kills	CV of the net reproductive rate	CV of N_0			
		0	10	20	40
0	0	0	4.7	9.5	19.2
	40	2.2	5.3	9.8	19.3
10	0	1.4	5.0	9.6	19.2
	40	2.7	5.5	10.0	19.4
20	0	2.9	5.6	10.0	19.3
	40	3.7	6.0	10.3	19.5
40	0	5.6	7.5	11.2	20.0
	40	6.2	7.8	11.4	20.2
60	60	9.3	10.5	13.4	21.3
	100	15.5	16.2	18.2	24.7

the variance of N_0 tends to completely dominate the variance of N_t because of the assumed independence of the kill estimates. Table 5 gives the CV for the back estimated population size of dolphin in 1959 for a range of CV for the different parameters involved in the estimate of N_{15} . As can be seen in this table, unless the variance of N_0 is near zero or unless the CV of the kill and reproductive vectors are extremely large ($>60\%$), the CV of the back estimate does not exceed the CV of N_0 .

Comparison of Equations (2) and (3).

A comparison of the estimated back abundance as calculated by the simpler model [Equation (2)]

TABLE 6.—Comparison of the back estimate of the abundance of bridled dolphin as calculated by the basic model [Equation (3)] and the simpler model [Equation (2)].

Year	Simple model ($\times 10^6$)	Basic model ($\times 10^6$)	Simple/basic
1974	3.500	3.500	1.000
1973	3.485	3.483	1.001
1972	3.624	3.617	1.002
1971	3.670	3.659	1.003
1970	3.850	3.835	1.004
1969	4.062	4.046	1.005
1968	4.115	4.093	1.005
1967	4.214	4.190	1.006
1966	4.412	4.386	1.006
1965	4.640	4.612	1.006
1964	4.840	4.811	1.006
1963	4.934	4.905	1.006
1962	5.021	4.991	1.006
1961	5.467	5.437	1.005
1960	6.001	5.971	1.005
1959	6.130	6.100	1.005

and the basic model [Equation (3)] for the dolphin population examined here is given in Table 6. The simpler model always gives a slightly higher estimate for the size of the back projected population but the increase in the estimate is always $<1\%$. The sensitivities of the two models are nearly equivalent. When the values for the parameters in these models deviate as much as 50% the difference between sensitivities of the two models is $<1\%$. The approximate variances of the back estimates of the two models are also similar.

That the difference between the original and the simpler model is small can be shown by analytically comparing the two models. If the projections are made only 1 yr into the past, the ratio of the estimate from Equation (2) to the estimate from Equation (3) is

$$1 + \frac{0.5R_1K_1}{N_0 + K_1 + 0.5R_1K_1}.$$

Only if the value of R_1K_1 is large relative to $N_0 + K_1$ can this ratio deviate significantly from 1. This is only possible if R_1 is relatively large. The general formula for the ratio of the two models is

$$1 + \frac{\sum_{j=1}^t 0.5K_jR_j \left(\prod_{h=1}^j (1+R_{h-1}) \right)}{N_0 + \sum_{j=1}^t 0.5K_j \left(\prod_{h=1}^j (1+R_{h-1}) \right) + \sum_{j=1}^t 0.5K_j \left(\prod_{h=1}^j (1+R_h) \right)}.$$

As in the case for projecting back only 1 yr, it can be seen that unless the R_jK_j terms are large relative to N_0 and unless the net reproductive rate is also large, the ratio of the two models will be close to 1.

DISCUSSION AND CONCLUSIONS

The results of this analysis indicate that errors in the input parameters do not compound in this procedure for estimating historical abundance. In fact, a systematic bias in the procedure for the estimation of a single set of parameters (either N_0 or R_i 's or K_i 's) always induces a bias in the back projected estimate which is less than the bias of the estimated parameters. This conclusion follows directly from the linear or near linear relation between S_t and n , k , or r with small rates of change. Moreover, the effects of bias in two or more sets of parameters are nearly additive. The interaction effects of bias in estimates of kills, net reproductive rates, and the initial number tend to

be small or nonexistent. This will be globally true for the relationship between k and n , but will be true for the relationship between k , r , and n only when the net reproductive rate is small. The relative importance of bias in K_i 's, R_i 's, or N_0 on N_t depends upon the actual values of the parameter. In the bridled dolphin example, after 15 yr, the back estimates were most sensitive to bias in the kill estimate, slightly less sensitive to bias in N_0 , and considerably less sensitive to bias in the net reproductive rate. However, the importance of bias in N_0 will diminish with the number of years in the back estimate with a proportionate increase in the importance of bias in the kills.

The sensitivity analysis developed in this paper will include the extremes of a complete sensitivity analysis of the model. The values for $S_i(0,k,0)$ are limiting values to a complete sensitivity analysis of the individual elements of the kill vector on N_t . Similarly $S_i(0,0,r)$ is a limit to complete sensitivity analysis of the individual elements of the net reproductive rate. Given the additivity of S_i with respect to n , r , and k , the surface $S_i(n,k,r)$ contains the extremes of a sensitivity analysis in all $2t+1$ dimensions. If in fact the elements within the kill vector and within the reproductive vector are highly interdependent (as is the case for the data used here), then the sensitivity analysis used to look at the effects of bias in this paper approaches a total sensitivity analysis of the back projected estimate given these constraints.

The variance approximations also indicate that variability in the parameter estimates does not result in compounding uncertainty in the back projected estimates. When estimates of the parameters are independent and the net reproductive rate is low, the CV of the back estimate will be smaller than the CV of the input parameters. In our example if all the CV's were equal, the variance of N_0 would make the largest contribution to the estimated variance of N_t . In general this will be true as long as the kills in any one year do not approach the initial abundance. This is a direct consequence of the basic additivity of the model when the net reproductive rate is small.

In Smith and Polacheck (see footnote 4), an alternative probability structure was considered in which the elements within the kill vector and within the net reproductive rate vector were highly interdependent. In this situation, the vari-

ance of N_t is not completely dominated by the variance of N_0 . The variances of N_t calculated using this interdependent probability structure are larger than the variances presented here in which all the parameters are assumed independent. However, the CV of N_t for the dolphin data within this interdependent probability structure is still less than the CV of the parameters if all parameters have equal CV. It appears that even in the situation in which a high degree of interdependence exists within the kill estimate or the net reproductive estimates, the variability in the parameter estimates does not induce compounding uncertainty in the back projected estimate.

The comparison of the results from the basic model [Equation (3)] with the simpler model [Equation (2)] indicate that there are no significant differences between the two models as long as the net reproductive rate is small. Thus it appears that there is no reason to favor the more complex model over the simpler.

In conclusion, it appears that this back projection procedure (either model) has reasonable statistical properties, at least when the net reproductive rates are small. However, Equation (1) is a simplified description of how the abundance of a population changes through time, especially in not accounting for changes in age structure. The authors feel that caution should be used in applying estimates from this procedure to the management of long-lived species since changes in the age structure for long-lived species are likely to be important.

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APPENDIX I.—Expressions for the variance components of N_t .

Expression for the right hand terms of Equation (9) are:

$$V(N_0) \left(\frac{\partial N_t}{\partial N_0} \right)^2 = V(N_0) \left(\frac{1}{\prod_{j=1}^t (1+R_j)} \right)^2 \quad (i)$$

$$\sum_{j=1}^t V(K_j) \left(\frac{\partial N_t}{\partial K_j} \right)^2 = \sum_{j=1}^t V(K_j) \left(\frac{1 + 0.5R_j}{\prod_{h=j}^t (1 + R_h)} \right)^2 \quad (ii)$$

$$\sum_{j=1}^t V(R_j) \left(\frac{\partial N_t}{\partial R_j} \right)^2 = \sum_{j=1}^t V(R_j) \left(\frac{N_{j-1} + 0.5K_j}{(1 + R_j)^2 \prod_{k=j+1}^t (1 + R_k)} \right)^2. \quad (iii)$$

APPENDIX II.—Coefficient of variation of a sum of random variables.

The following is a proof that the coefficient of variation of a sum of two independent random variables is smaller than the greatest CV for either of the random variables if the expected value of the random variables is greater than zero.

If A and B are independent random variables such that

$$\begin{aligned} E(A) &= a > 0 \quad E(B) = b > 0 \text{ and} \\ CV(A) &= \frac{\sqrt{V(A)}}{a} \geq \frac{\sqrt{V(B)}}{b} = CV(B) \end{aligned}$$

then

$$\frac{V(A)}{a^2} \geq \frac{V(B)}{b^2},$$

$$V(A)b^2 \geq V(B)a^2,$$

$$V(A)(b^2 + 2ab) > V(B)a^2,$$

$$V(A)(b^2 + 2ab) + V(A)a^2 \geq V(B)a^2 + V(A)a^2$$

$$V(A)(a + b)^2 \geq [V(B) + V(A)]a^2,$$

$$\frac{V(A)}{a^2} > \frac{V(B) + V(A)}{(a + b)^2} = \frac{V(A + B)}{[E(A + B)]^2},$$

$$CV(A) > CV(A + B).$$

**SPORT FISHING IN HAWAII
GUAM AND AMERICAN
SAMOA**

**WITH CHARTS TO FISHING
GROUNDS
AND
AN ILLUSTRATED GUIDE TO
PACIFIC FISHES**

by
JAMES L. SQUIRE, JR.
AND
SUSAN E. SMITH

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Publisher's Preface

This handbook to sport fishing in the Hawaiian Islands, American Samoa & Guam, with associated fishing ground charts and guide to marine game fishes, is selected for the convenience of fishermen from the Angler's Guide to the United States Pacific Coast (first published by the U. S. Department of Commerce.)

All entries in the marine game fishes has been left intact as fishes on the American West Coast are of interest to sport fishermen in Pacific Island Waters. The introduction to the original work has been slightly reduced by omitting sections referring to sport fishing outside of the areas covered in the charts.

CONTENTS

Introduction	v
Hawaiian Islands	2
American Samoa	12
Guam	14
Marine Game Fishes	17
Glossary of Terms	46
Index to Common Names of Fishes	48
Acknowledgements	53

Introduction

While there are millions of individual fish in the ocean and bays, the obvious problem facing the marine sport angler is how and where and when to catch them. Anglers who have a "local knowledge" of the seasons and locations of good fishing areas usually are the more successful ones, but most realize that pinpointing the exact location, season, and time for catching a certain species of fish is impossible. This is due to seasonal variation in the geographical distribution and quantity of stocks of fish available, which, in turn, is a result of changes in the total marine environment (temperature, salinity, food, etc.), and the biological success of each species in the competition for survival. Even so, certain species usually are taken in generally well defined fishing areas: some may be taken only during a certain seasonal period while others may be present throughout the year.

The purpose of this Guide is to provide a general source of information on those areas that are more frequently fished and the species of fish that are commonly taken. Accompanying each chart is a general description of the chart area, and notes that supplement the chart information concerning some of the common game fishes and their availability to the angler.

It is important to realize that marine game fishing is the only segment of the U. S. fisheries that has grown rapidly during the past 15 years. In 1960 the first national marine angling survey was made. It reported an estimated 1.4 million marine anglers along the west coast from the Mexican border to Alaska catching over 79 million fish. By 1965 the number of marine anglers had grown to almost 2 million (1,977,100) and the catch to over 87 million fish. The 1970 survey showed over 2 million (2,205,000) west coast marine anglers who caught over 61 million fish. Thus, during the past decade, the number of west coast anglers has increased 64%; however, the number of fish caught as reflected in the 1970 survey has not kept pace with the increased angling pressure. This increase in angling pressure is to be found throughout the central and eastern Pacific, with a 34% increase in southern California, which has 40% of all marine angling along the west coast. A 47% increase was found from central California northward into Alaska, an area which accounts for 60% of all west coast fishing.

Effective long-range planning for marine game fish conservation programs and associated research activities must be based on a thorough knowledge of the scope and magnitude of the recreational fishery resources; seasonal distribution of fish; the operating sport fishery and its fishing locations; the location, type and number of fishing facilities available; and information on the values that anglers attach to the various facets of the sport.

TYPES OF FISHING

Pacific marine game fishing is centered near the coastal population centers. An abundance of desirable game fish is usually available along all coasts in the ocean, bays, and brackish-water areas, depending on the place and season of the year. Over 300 species are commonly taken by marine anglers who fish the west coast and Pacific Islands: in addition, they incidentally catch many other species.

The sport angler has five types of "fishing" — pier fishing, rock or jetty fishing, surf or bank fishing, private boat fishing, and sport boat (party or charter boat) fishing. The type of marine environment fished usually dictates what species are most likely to be caught. The marine angler must take this into consideration by use of suitable equipment and careful selection of bait or lure to achieve the greatest chance for success.

A diversity of fishing gear is used by the Pacific angler, with conventional hook and line being the most common method of fishing in all areas.

CHOOSING A FISHING AREA

If you are unfamiliar with an area, there are a few basic criteria that should be used in selecting a place to try your luck. Knowledge of hydrographic conditions (tidal flow, bottom types, and depths) is most important whether you are fishing in the open ocean, nearshore, surf zone, tidal inlets, bays, or in the intertidal portion of a river. On the open ocean, sea state is another important factor in fishing. Many pelagic species that frequent the surface are usually found at greater depths when the surface is rough. Weather is a particularly important factor, especially in the ocean. Where weather is more favorable for offshore fishing, we usually find a greater number of offshore anglers.

In fishing offshore for marlin, water color and temperature are important factors. Changes in these factors are good indicators of changes in water mass, and it is in the vicinity of these changes that concentrations of the larger predators are often found. Along edges of changes in water temperature and color sometimes can be found higher concentrations of forage animals — plankton and small fish. These smaller animals attract the larger predator fish, making an area with a temperature or color discontinuity a favorable place to explore. Locations near schools of forage fish often have good fishing potential. These frequently are found by observing seabirds swooping down on forage fish driven to the surface by larger predator fish. Sometimes yellowfin tuna and marlin are found around schools of porpoise, and trolling nearby may be productive.

Along shore, water depth frequently can be determined by color, the darker blue color indicating a deeper area. These deep spots or holes, drop offs, and open channels are all good spots for surf or shore anglers to investigate. In fishing the surf, wave action is most important in evaluating a

good fishing spot; as a wave proceeds toward the shore, it will usually crest and break over a shallow spot, either the sand beach itself or an offshore bar. If the wave breaks some distance from shore over a submerged sandbar and the water becomes smooth again before slightly breaking on the beach, this indicates a depression or hole on the inside of the bar — a likely spot for surf fishes. If rocky outcroppings are observed immediately offshore along a sandy beach, casting to a point close to the rock can be productive since larger fish tend to congregate around such locations. The same is true for offshore reefs, kelp beds, or wrecks. These habitats provide shelter or protection as well as a ready food supply for game fishes, which eat the abundant small organisms attached to the solid substrate and the baitfish frequently found nearby.

Rocky shores usually are productive fishing areas; however, many anglers are reluctant to fish these places because of the possibility of losing their terminal gear of sinkers and hooks. Careful selection of a fishing spot off a rocky point or over sharp drop offs to deep water which may have a smooth bottom could produce results. Although a cautious approach should be taken in testing such an area, after discovering good fishing in a rocky location you may have found your own exclusive fishing spot.

Fishing results in bays are highly variable. Usually the best spots are near the entrances, in or adjacent to the main tidal channels. Fishing in the entrance from a boat can be productive either by trolling (usually against the tide), casting with the tide, or drift fishing with the tide. Tidal fluctuations in bays markedly affect fishing in the nearshore area or over the tidal flats. Water current velocities and patterns created by tidal flow in turn affect the movement and availability of food material for all bay fishes. Many shallow areas are evident, and some are exposed at extreme minus tides. When the tide is high these areas are covered, and predator fish can move over the tidal flats to feed on small invertebrates that live on the bottom. On an ebbing or outgoing tide, good places for fishing are usually found in channels or about the mouths of tidal sloughs that drain the tide flats, or at any narrow channel or creek mouth at the point it empties into a bay.

In bays as well as in the ocean, logical spots for fishing in your area may be found on the marine nautical charts issued by the National Ocean Survey. These navigational charts show channels and depressions and sometimes show rough or rocky-reef areas. A good marine angler can determine areas that may have good fishing potential by consulting these charts, and if you plan to fish from your own boat, knowledge of the bottom topography is essential for normal navigation.

Another easy method of gaining knowledge of the better fishing sites is to follow those sport anglers who know where to fish. Good fishing areas attract fishing boats and concentrations of anglers. The activities of commercial sport fishing boats are among the most reliable indicators of good fishing spots. Professional sport fishing boat skippers keep in constant contact by

radio with other boats concerning fishing conditions, and they are the experts in the offshore fishing business. For this reason a great deal of knowledge about fishing techniques for different species and fishing locations can be obtained by fishing from a commercial sport fishing boat. Records indicate that in most cases catches are above average for these boats, and their equipment will get you to the fishing grounds and back with speed and safety. Once the fishing grounds are reached, all necessary bait (live bait in many cases), tackle, and instruction on equipment and techniques are available to you.

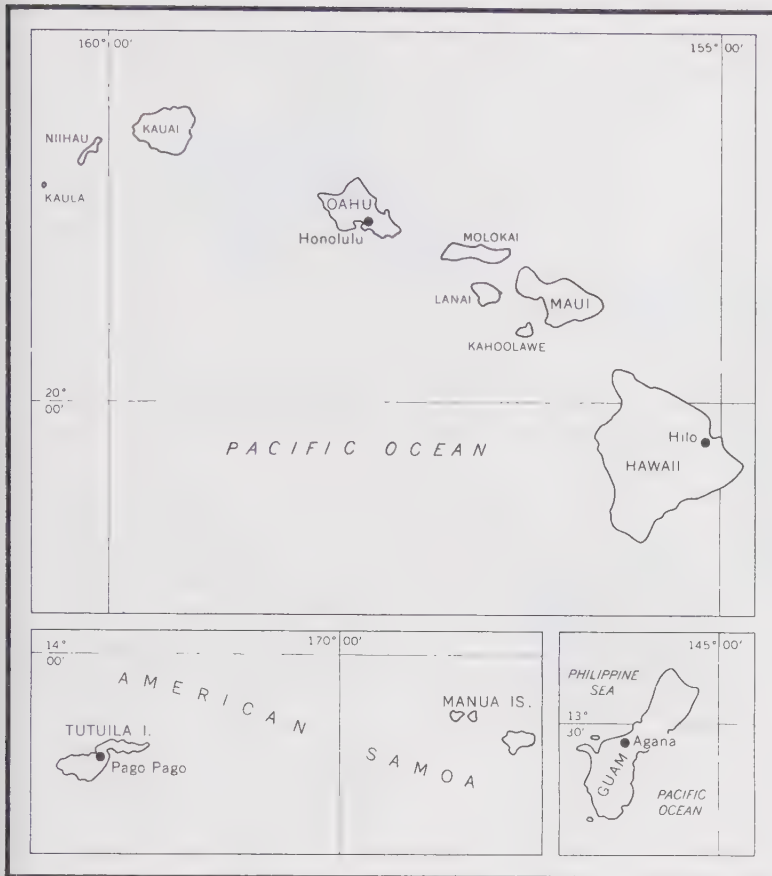
Finally, for more specific knowledge about fishing in a particular area, one of the most logical places is the local bait and tackle store or sporting goods supplier. Local fish and game wardens usually are most helpful, and of any group of individuals, they are probably most aware of seasonal fishing opportunities. Above all, before fishing any area always be sure to consult your State fish and game department for local regulations concerning current laws.

JAMES L. SQUIRE, JR.

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PACIFIC ISLANDS

The following pages describe marine game fishing around the tropical islands of Hawaii, American Samoa, and Guam. The Hawaiian Islands rise out of the central Pacific Ocean near the margin of the tropics, while American Samoa lies below the equator approximately 2,600 miles south of Honolulu. Guam, the largest and westernmost territory of the United States, is located in the western Pacific Ocean less than 1,700 miles south of Tokyo, Japan. Although widely separated geographically, these islands all fall within the boundaries of a large region characterized by a distinct marine fauna—a region that extends from East Africa across the Indian Ocean into the central Pacific Ocean. Thus many similar or identical species occur in Hawaii, American Samoa, and Guam.

All of these islands are volcanic in origin with the sea bottom plunging fairly rapidly away from shore, and in many locations excellent deep-sea fishing opportunities are available within a relatively short distance from port. Some of the billfish and tuna grounds have produced record-sized fish and earned a worldwide reputation in big-game fishing

circles. But although the glamour and excitement of deep-sea fishing draws many to the offshore grounds, much of the fishing conducted about the islands is for the great variety of smaller tropical fishes found over inshore reefs and along rocky and sandy shores. The most sought-after fishes are not necessarily the largest or the ones with the best fighting ability—many islanders judge the value of a fish by its taste and by the traditional values attached to catching it and preparing it for the table.

Visitors should always first check locally about the area they plan to fish unless accompanied by a professional skipper or guide. If you intend to fish from shore, ask about surf conditions, accessibility, and restricted areas. Double check the edibility of your catch, particularly in American Samoa and Guam, where a few species are reported to be poisonous. Those known or suspected to be poisonous are discussed in the accompanying text and in the section on Marine Game Fishes of the Pacific Islands.

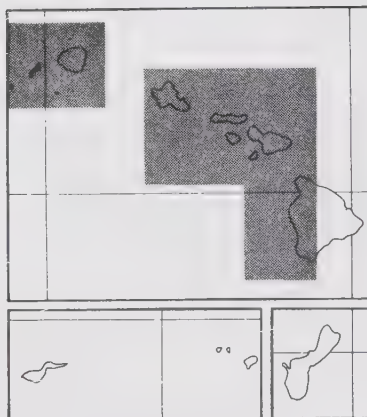
HAWAIIAN ISLANDS

The beautiful islands of our 50th State, Hawaii, are situated in the north Central Pacific Ocean over 2,000 miles southwest of mainland North America. The Hawaiian archipelago comprises eight major islands and a number of rocky islets and small coral islands. The larger islands are actually the high peaks of an undersea chain of volcanic mountains and rise steeply and majestically out of the deep clear-blue waters of the Pacific. Geologically, the islands were formed west to east, the youngest island being the island of Hawaii, which still has active volcanoes. The oldest are the tiny coral sand islands at the westernmost tip of the chain.

The climate is largely influenced by the northeast trade winds that travel over the cool, westward flowing North Equatorial Current, and then are affected by the high elevations and contours of the islands. As a result, the islands have a relatively cool, wet windward side and a warm, dry leeward side, and there is wide variation in temperature, wind, and rainfall according to locality. In general, temperatures range from 56° to 90°F, are lower from November through April, and mild to warm the rest of the year. Warmest months are July, August, and September when temperatures may reach 80° to 90°F. Occasionally a southerly or "Kona" wind brings mugginess to the islands and rain to the leeward coasts.

The population is unevenly distributed; 82% of the people live on Oahu, and three-quarters of these in the city of Honolulu. Hawaii, the largest island with six and a half times the land area of Oahu, has only 8% of the population.

The islands of Hawaii offer a variety of excellent year-round fishing—deep-sea, inshore, and shoreline fishing.



34/Hawaii Big Game Fishing

Hawaii's blue marlin and tuna grounds are world famous, and the professional skippers and crews that fish these waters are among the most experienced blue-water anglers in the world. Charter boats provide full equipment and operate year-round on a nonscheduled basis. Advance reservations should be made with individual boat operators or with charter services. International Game Fish Association's scales and weighmasters are available on all the main islands.

The major trolling grounds for Hawaii's sport fishing fleet are shown on Chart 34. Most fishing is done off the calmer leeward coasts of the islands. The windward coastal waters and the channel areas between the islands are just as productive for big

game fish, but the seas in these blustery areas are often rough and tend to discourage most anglers. Fishes that are taken by trolling include blue, black, and striped marlins (all called "a'u" by the islanders), 'ahi (yellowfin tuna), aku (skipjack tuna), mahimahi (dolphin), ono (wahoo), kawakawa (little tunny), and kamanu (rainbow runner or Hawaiian salmon). Most trolling occurs in water 1,000 fathoms or less; although off the Kona coast of Hawaii, boats may fish over water up to 2,000 fathoms or more deep in search of marlin and tuna.

There are two basic types of fishing strategies—area fishing and ledge fishing. Anglers who "fish the area" work over a known productive fishing ground such as Penguin Bank or the "Chicken Farm," watching for flocks of seabirds which feed on the baitfishes that marlin and large tuna chase to the surface. Ledge fishing involves trolling along submarine shelf areas where marlin, tuna, and other smaller fish are known to concentrate and feed. Aside from being excellent marlin and tuna areas, these precipitous ledges also produce impressive numbers of ono and kahala (amberjack), as well as the large deepwater snappers which are caught handlining on the bottom.



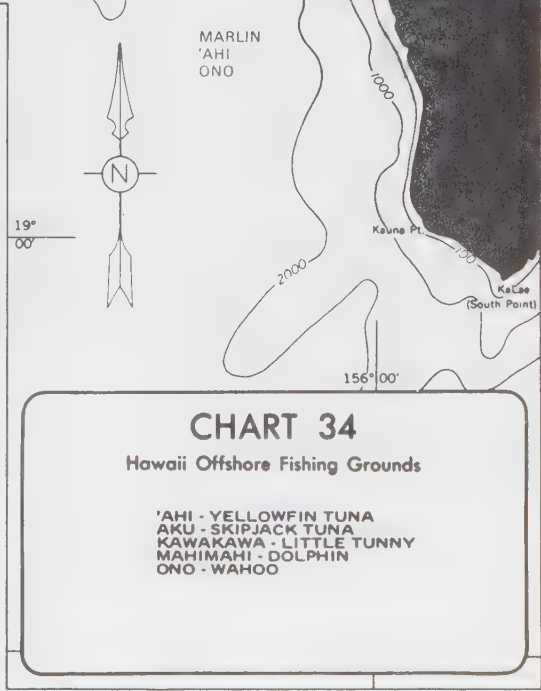
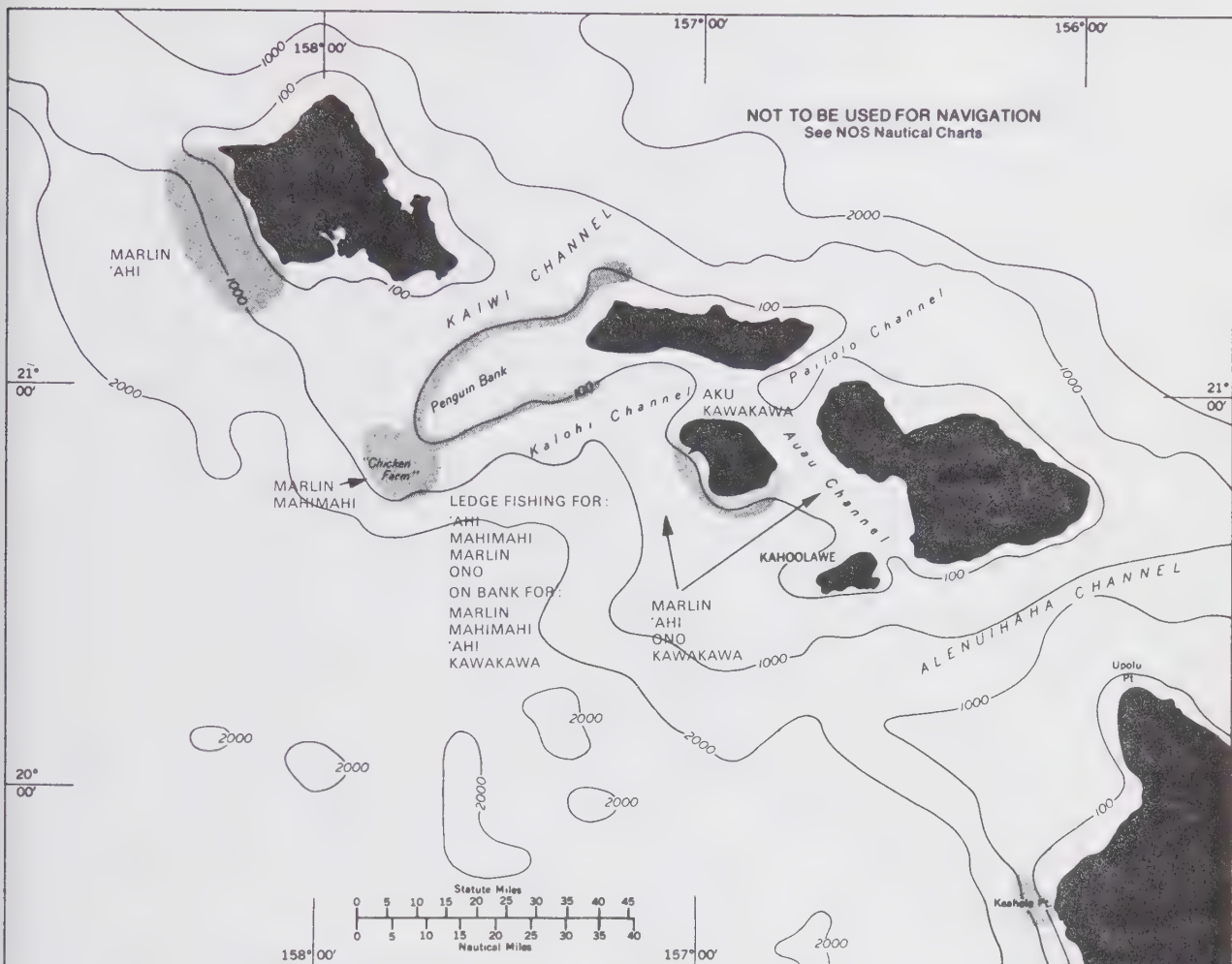
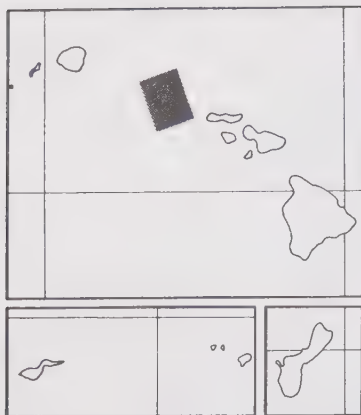


CHART 34

Hawaii Offshore Fishing Grounds

'AHI - YELLOWFIN TUNA
AKU - SKIPJACK TUNA
KAWAKAWA - LITTLE TUNNY
MAHMAHI - DOLPHIN
ONO - WAHOO



35/Oahu

Oahu (Chart 35) is the political and commercial center of the Island State, where the bustling capital city of Honolulu is located. It is here that most of Hawaii's people live and work.

The island is formed by two rugged parallel volcanic mountain ranges separated by a wide valley carpeted with sugarcane and pineapple. Many shore recreation spots and scenic views are within easy access along highways that circle and cross the island.

OFFSHORE FISHING

Honolulu's Kewalo Basin, only a 5-minute drive from the Waikiki hotel district, has fine fleets of deep-sea cruisers. Charter boats fish close-in and offshore for many different types of game fish—marlin, 'ahi, mahimahi, kawakawa, ono, and sometimes the deepwater snappers—depending on what is running. Marlin have been caught within a mile of the harbor. Honolulu boats often fish from Penguin Bank to the east of the island or work from the western or leeward shore along Barbers Point to Kaena Point off the Waianae coast. Penguin Bank is noted for large schools of small tuna and mahimahi as well as marlin and ono. The Waianae coast offers the comfort of fishing in the calm lee of the island and a promise of exceptionally large marlin and yellowfin tuna ('ahi). Charter boats out of Pokai Bay Boat Harbor also fish this area. On the windward coast, charters are available at Heela Boat Harbor in Kaneohe Bay, and when weather permits, there is good marlin fishing along the 100-fathom drop off between Makapuu Point and Mokapu Point.

NEARSHORE AND SHORELINE FISHING

Fishing from shore is probably the most popular way to fish throughout

the Pacific Islands. Getting to shore is relatively easy in most places, and the cost of this type of recreation is nominal. A variety of methods are used—pole and line, netting, spearing, and trapping. Only a few places in Hawaii rent fishing tackle, but all of the islands have sporting goods stores where inexpensive gear can be purchased.

Heavy bait-casting gear is used mainly for ulua, an island term for large-sized jacks. These fish are highly prized by shore anglers and some are reported to reach 5 feet long. Ulua are found around rocky headlands and points, usually in turbulent water. Some of the best fishing spots for ulua on Oahu are Koko Head, Bamboo Ridge (north of Hanauma Bay and to the south of the Blow Hole), Diamond Head, Makapuu Point, and Kaena Point. This type of fishing can be dangerous for the beginner because of the rugged nature of the terrain in most ulua fishing areas. Access to some of the better fishing spots is sometimes difficult, and the surf can be treacherous—reports of anglers being swept from the rocks by waves are not uncommon.

Young jacks, called "papio," are favorite light tackle quarry for pier and shoreline anglers. Papio are caught all around the island, being most abundant from August to November. Another member of the jack family, the akule, is also a popular light tackle fish. Most pole fishing is for young akule or "hahalalu" (often pronounced simply "halalu"), which are caught in bays and harbors, such as Pokai Bay and Haleiwa Harbor, and in Honolulu Harbor by pier fishing under lights. Hahalalu are caught mostly at night, as are a variety of other inshore fishes.

Some fishes that are active at night—wekes, aholehole, and 'ama'ama—are caught by "torch fishing." On calm dark nights when the tide is low, persons armed with spears or hand nets wade out over the reef carrying lights to locate marine animals. Years ago, torches were made from dried coconut leaves, but now gasoline lanterns and battery-powered lights are used. Lobsters and "squid" (octopus to mainlanders) are also taken torch fishing.

The "hukilau" is another traditional island fishing method. It involves a group of people. A large surround net is used to encircle the fish, usually in protected waters. Once the net is set in place everyone pulls on the two end ropes, forcing the fish into the net as it is drawn into shallow water. Usually all kinds of fishes are caught with the hukilau net, and custom dictates that anyone who wets his feet during netting be given a portion of the catch.

Some of the popular shore fishing

FACILITY NUMBER
SPORT BOAT OPERATION
PIER FISHING
SKIFF RENTALS
LAUNCHING
JETTY FISHING
LOCATION

1	● ● ● ●	Keehi Boat Basin
2	● ● ● ● ●	Kewalo Basin
3	● ● ● ●	Ala Wai Boat Harbor
4	● ● ● ● ●	Maunaloa B. Beach Pk.
5	● ● ● ● ●	Kailua Beach Park
6	● ● ● ● ●	Heela-Kea Boat Harbor
7	● ● ● ● ●	Kahana Bay
8	● ● ● ● ●	Haleiwa
9	● ● ● ● ●	Pokai Bay Boat Harbor

and torching areas are shown on the map. In Honolulu Harbor there is pier fishing for 'oama, halalu, and maomao. The shallow reef around Honolulu Airport is a favorite location for netting 'ama'ama; spinning for papio and 'o'io; and, on calm nights, torching for weke. Parts of Waikiki Beach are good for torch fishing, especially for "squid" (octopus). There is also fishing from shore for aholehole, papio, 'ama'ama, and awa along the Ala Wai Canal that cuts through the Waikiki Beach district. Along Waimanalo Beach, 'o'io and weke are caught from shore, and moi are taken near the mouths of creeks emptying into Waimanalo Bay.

Farther north, Kaneohe Bay has netting for surgeonfish (manini and kala), 'ama'ama, akule, awaawa, and awa. Kaneohe Bay is also one of the better areas for octopus or "squid," and underwater spearing for kumu, manini, palani, and weke-ula. 'Omaka are abundant seasonally, and 'aweoweo on occasions enter the bay in great numbers. All along the north-eastern coast there is shore casting over reef-and-sand bottom for papio and weke; over sand bottom for moi and 'o'io; and cast netting and gill netting inside of the reef for surgeonfish, 'ama'ama, and akule.

In Haleiwa Bay, hahalalu school in great numbers in late summer, and many are taken by pole fishing from shore. Hahalalu and 'opelu are taken in the surf along the coast north of Waianae; 'o'io and ulua are caught off the shores around Nanakuli; moi and

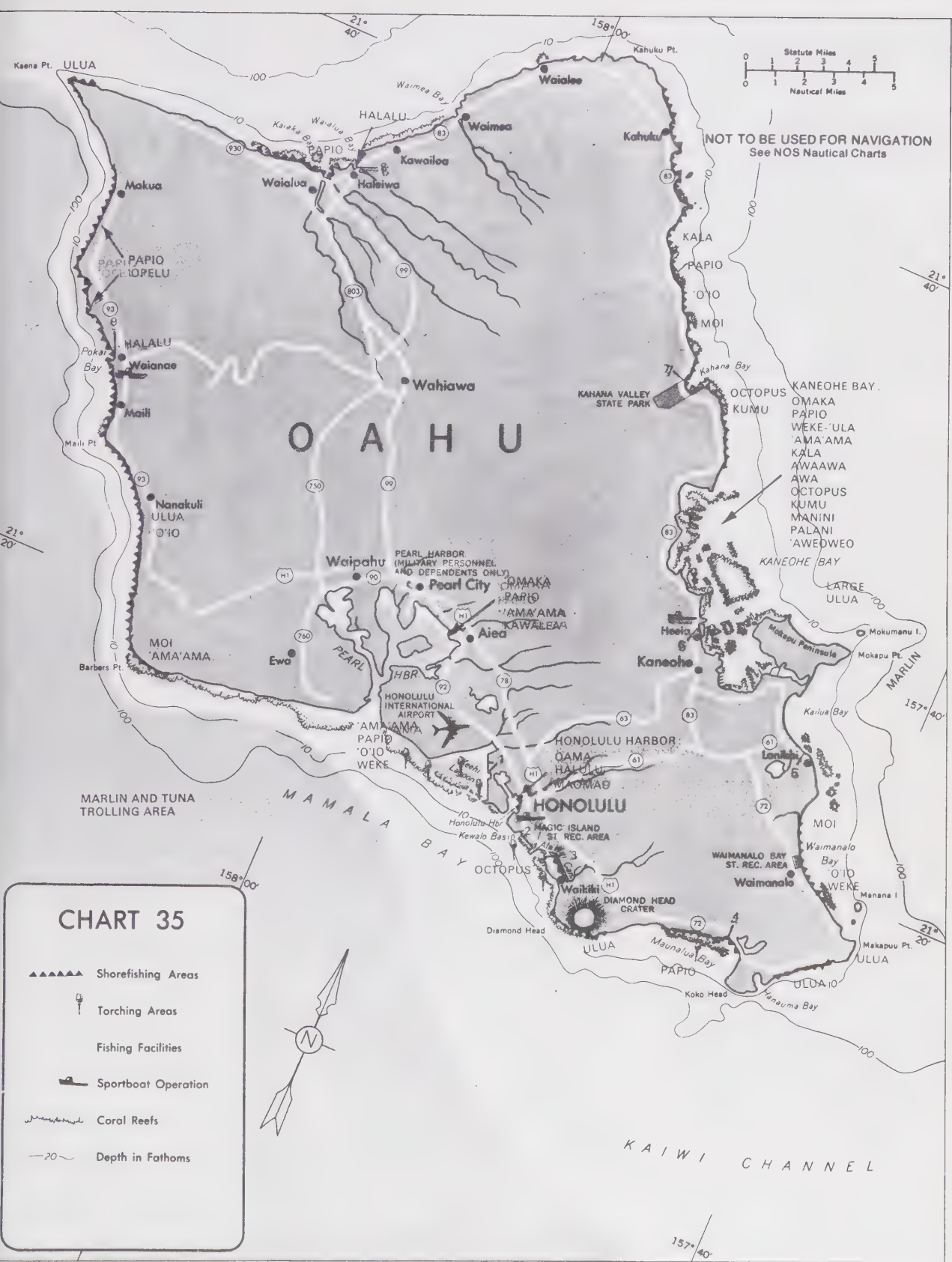


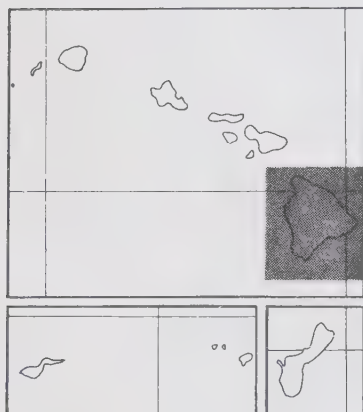
CHART 35

- ▲▲▲▲ Shorefishing Areas
- 🔥 Torching Areas
- 🐟 Fishing Facilities
- 🚤 Sportboat Operation
- 🪸 Coral Reefs
- 20— Depth in Fathoms

NOT TO BE USED FOR NAVIGATION
See NOS Nautical Charts

'ama'ama are taken by netting and shore casting around Barbers Point. Fishing in Pearl Harbor is restricted by the military, and it is fished by service personnel and their dependents. The harbor is good for cast netting 'ama'ama; pole fishing for papio, 'omaka, nehu, and palani; and spin-fishing with lures for kawalea.

There is a considerable amount of small-boat fishing in reef-protected areas and in bays and harbors around the island. All facility locations indicated on the map have launching ramps, except Kewalo Basin. 'Omaka, 'aweoweo, menpachi, papio, and weke-'ula are caught from boats in Kaneohe Bay, and hahalalu sometimes are taken by skiff anglers in Haleiwa Bay. Large ulua are taken in the area north of Mokapu Peninsula, and boats bottom-fish for 'omaka in Pearl Harbor.



36/Hawaii

The island of Hawaii (Chart 36), often referred to as the "Big Island," contains two-thirds the land area of the entire island chain. It consists of five volcanic mountains about 20 miles apart and linked together by saddles, 3,000 to 7,000 feet high, formed by overlapping lava flows. Along the northeast coast, the island takes the full brunt of the northeast trades and is exposed to heavy rains. The rest of the island is rather dry and arid owing to the spongelike porosity of the rocks and lack of rain on the leeward side. All around the island, water depth plunges dramatically and rapidly away from shore.

OFFSHORE AND NEARSHORE FISHING

Most offshore game fishing occurs on the calmer leeward or Kona coast during spring, summer, and fall. In winter, especially during January,

there is little fishing activity because of rough seas, but fishing usually picks up again in February. Blue marlin can be caught all year, but are most abundant from June through October. Striped marlin appear to be more abundant during times when blue marlin are least abundant (during winter and early spring), and are not caught by sports anglers in as many numbers as the blues. Best time for 'ahi is November through April. Aku are taken all year, but best catches are made in the summer. Ono are most abundant from April through August.

The Kona coast is famed for its smooth, clear water and ideal fishing conditions. It is also famous for the Hawaiian International Billfish Tournament, which is staged every summer at Kailua-Kona. Anglers from all over the world come to fish the waters of the Kona Coast, where several marlin over 1,000 pounds have been landed in recent years. The most popular grounds fished by the charter fleet are off Keahole Point—less than an hour's run from Kailua-Kona. Boats also fish along the entire leeward coast as far south as Kauna Point in search of marlin and tuna.

Farther inshore, 'ahi and ono are taken in good numbers by trolling over the steep 100-fathom ledge. This drop-off area also is good for handlining onaga and kahala. From about 40 to 100 fathoms there is handlining and netting for akule, 'opelu, 'opakapaka, and some of the goatfishes or wekes—weke-'ula and moana. Nearshore out to about 50 fathoms deep, menpachi, manini, and moano are taken. The Kawaihae (Kohala) coast on the northwest side of the island is especially good for ono and 'ahi as well as other smaller game fishes. However, waters tend to get a little rough in the afternoon, when the wind usually picks up in this area of the coast. Boats based at Kawaihae often make the run down to "the grounds" off Keahole Point for marlin and tuna. When weather permits, overnight trips are made from the Kona area down to South Point for 'ahi, ono, and 'opakapaka.

The windward coast has limited offshore fishing by private boats based out of Hilo for marlin, 'ahi, ono, mahimahi, and kawalea. These grounds are fished only by experienced anglers familiar with the area—the extremely heavy swells and rough seas are not for the novice angler and boat handler. Akule, opelu, and ta'ape are taken farther inshore, and within the protection of Hilo Bay fishing is excellent for moi and other small game fishes.

SHORE FISHING

Although access is difficult, if not impossible, along much of Hawaii's

FACILITY NUMBER
SPORT BOAT OPERATION
PIER FISHING
SKIFF RENTALS
LAUNCHING
JETTY FISHING
LOCATION

1	● ●	Mahukona
2	●* ●	Kawaihae
3	●	Puako
4	● ●	Honokahau Harbor
5	● ●	Kailua-Kona
6	● ●	Keauhou B. Anchorage
7	●	Honaunau Bay
8	●**	Miloli
9	●	Kaulana Bay
10	●	Pohoiki
11	● ● ●	Hilo
12	●	Laupahoehoe
13	●	Kukuihaele

*Movers to Kailua occasionally.
**High tide only.

coastline, there are still many places where one can fish from shore. An assortment of fishes are taken: among them the most sought after appear to be large ulua and their younger offspring "papio"; the convict tang or manini; and young akule or hahalalu.

Hawaii's rugged coastline is particularly suited for ulua fishing. One of the best areas for ulua is at South Point, where black ulua are most abundant in the winter, and white ulua are caught year-round, dominating the catch in summer. Other good areas are Upolu Point, Kealakekua Point just north of Kealakekua Bay and the area south of the Bay, and all along the windward coast south of Hilo.

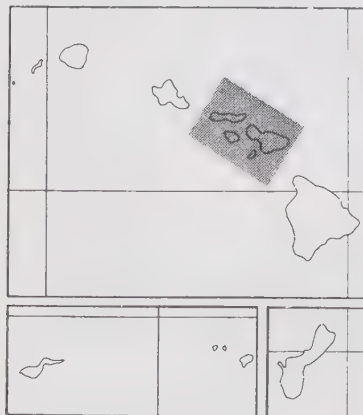
The small but tasty manini is a very popular shore fish on the island of Hawaii. They are caught all around the island—mostly by cast netters.

Papio are abundant and are caught pole fishing along the coast and in bays and harbors. Hahalalu are also taken pole fishing in bays and harbors, particularly at Hilo, Kawaihae, Honokahau, Kailua, and Keauhou.

Some of the more popular shore-fishing areas are indicated on the map. Along the leeward coast, 'ama'ama

and manini are taken from shore between Kawaihae and Puako. There is limited access over the lava fields south of Puako, but Honokakau Harbor and the coast south to Kailua offer some shore fishing. South of Kailua-Kona there is intermittent access to shore along the highway—some areas are privately owned. From about Keauhou south to Kealahou Bay the fishing is reported to be excellent, but access is difficult—only by way of a dirt trail about one-half mile south of Keauhou Bay. In most of Kealahou Bay, fishing is restricted, but to the south there is shore fishing for ulua, menpachi, and papio (about a 5-minute walk to the beach). A limited amount of shore fishing occurs near Hoopuloa and Milolii.

The windward or Hilo coast of the island has shore fishing along Hilo Bay for moi, and from the Hilo breakwater for moi, manini, hahalalu, weke, and papio. The area south of Lelewi Point is good for moi, manini, aholehole, uouoa, weke, 'o'io, and ulua. From around Kaloli Point south to Cape Kumukahi, large ulua are taken from shore as well as menpachi and some of the fishes mentioned above. Farther south at Opihikao, islanders fish for menpachi, manini, moi, 'o'io, papio, and ulua. Punaluu Harbor and Honuapo Bay have a limited amount of fishing for akule.



37/ Maui, Molokai, Lanai, Kahoolawe

This island group (Chart 37) was probably once a single island, but now is separated by channels 6 to 9 miles wide and up to 100 fathoms deep. The island of Maui is called "The Valley Isle" from the low-lying valley or isthmus that links the two volcanic mountains that form east and west Maui. It is the largest island of the

group and the second largest island in the Hawaiian chain. The windward or eastern side is a succession of gorges rich in lush vegetation, cascading waterfalls, and black sand beaches. The leeward or western side of the island is characterized by golden sand beaches, secluded coves, and very clear waters.

The island of Molokai also is formed by two volcanic mountains. Its windward side is very scenic with precipitous cliffs, rising sheerly 500 to 4,000 feet from the ocean, and indented by magnificent valleys. The leeward side is a patchwork of ancient fish ponds fringed with coral reef.

The islands of Lanai and Kahoolawe are both single mountains. Lanai, owned by the Dole Pineapple Company, is primarily a pineapple plantation. Kahoolawe is uninhabited and sometimes used as a target area by the U.S. Armed Forces.

OFFSHORE FISHING

Sport fishing boats are available for charter on Maui at the old whaling port of Lahaina, close to the Kaanapali Beach resort area. Most deep-sea fishing takes place in the triangle formed by the islands of Maui, Lanai, and Kahoolawe. Fishing around Molokai and Lanai can be arranged through Maui charter services. At the time of this writing, charters were also available on an intermittent basis out of the port of Kaunakakai on Molokai, but this should be checked with the charter services.

Boats out of Lahaina troll for mahimahi, kawakawa, ono, and blue marlin, or bottomfish for deepwater snappers and weke-ula. Most fishing is done in the protected lee of the islands, but during calm weather some boats venture out in the channel areas to bottomfish over the productive submarine ledges of the Pailolo Channel, the 100-fathom ledge where Auau and Kealaikahiki channels meet, and around the island of Kahoolawe. It is best to check with the Hawaii Division of Fish and Game about fishing around Kahoolawe; sometimes it is restricted during Naval operations. The area to the west of Lanai and Molokai is fished by privately owned vessels and the charter fleet out of Oahu.

INSHORE AND SHORELINE FISHING

Beaches, rocky points, and reefs along the coastlines of these islands offer excellent opportunity for spin fishing, surf casting, net fishing, and spearing. On Maui, skiffs can be rented at Lahaina for nearshore fishing along the Lahaina coast from Lipoa Point to Maalaea Bay along Highway 30.

FACILITY NUMBER
SPORT BOAT OPERATION
PIER FISHING
SKIFF RENTALS
LAUNCHING
JETTY FISHING
LOCATION

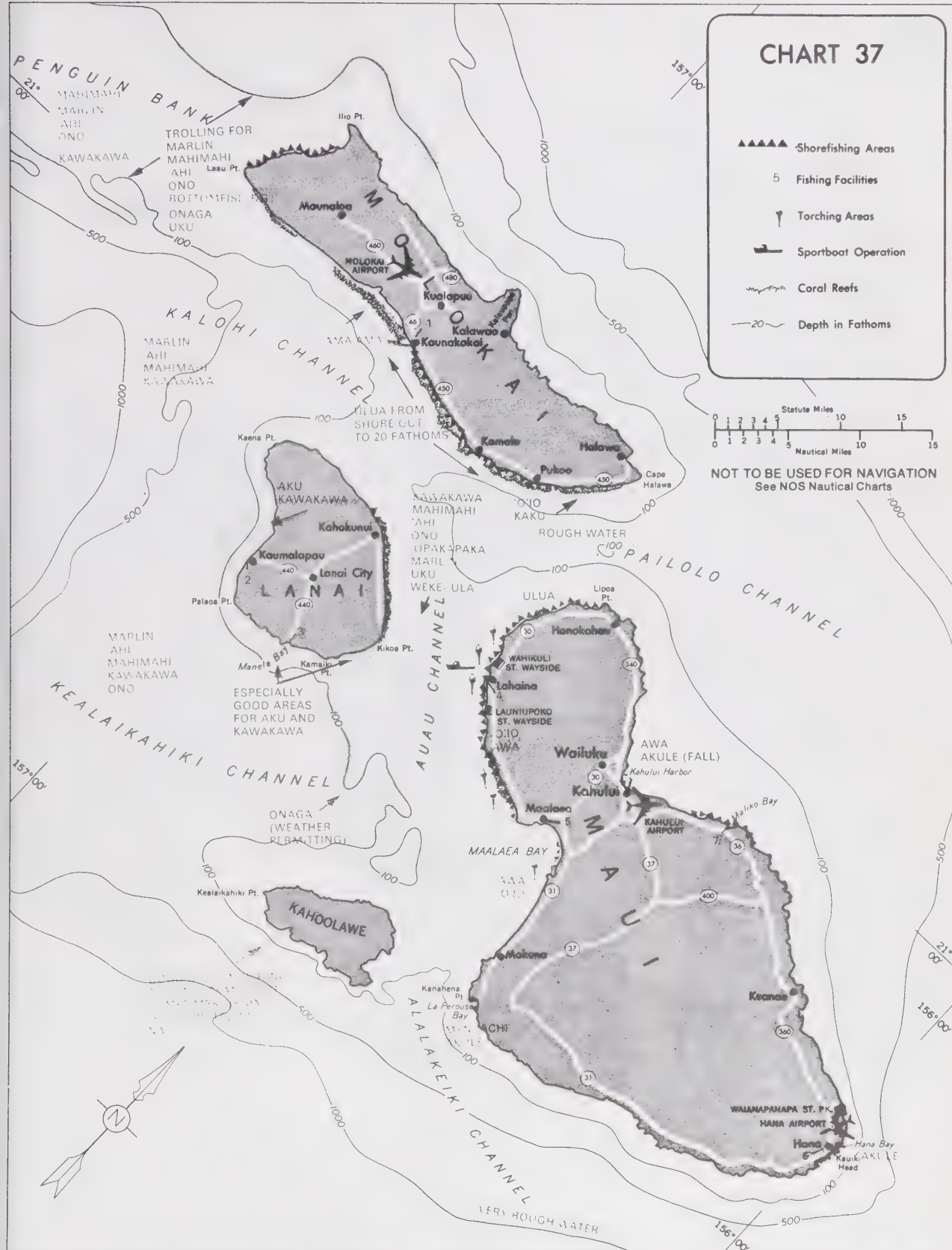
1	● ● ●	Kaunakakai, Molokai
2	●	Kaumalapau pier, Lanai
3	●	Manele Boat Hbr., Lanai
4	● ● ● ● ●	Lahaina, Maui
5	● ● ●	Maalaea Boat Hbr., Maui
6	●	Hana, Maui
7	●	Maliko Bay, Maui
8	● ● ●	Kahului, Maui

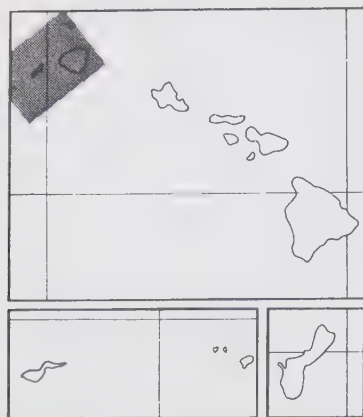
Perhaps Maui's most popular shore fish is the 'o'io (bonefish), which grows to a substantial size in Hawaiian waters. 'O'io and awa are taken from shore and skiffs along the Lahaina coast south to Maalaea and along the shore of Maalaea Bay and to the south. Large ulua also are taken along the Lahaina coast at the areas shown on the chart. On the eastern or windward side of Maui, awa and akule are caught in Kahului Bay during the fall; akule also are taken in Hana Bay. South of Hana Bay there is occasional shore fishing in winter for moi, aholehole, and manini. At the southwestern tip of the island at La Perouse Bay, akule, menpachi, and a wide assortment of reef fishes are taken from shore.

On Lanai, most shore fishing takes place on the northeastern side of the island, which is edged with luxurious coral reef. Kaumalapau Harbor has pier fishing and fishing for awa just outside of the harbor entrance.

On the island of Molokai, shore and skiff fishing for ulua is exceptional all along the leeward coast inshore of 20 fathoms. From Kaunakakai to Halawa there is fishing from shore for 'o'io, awa, and 'ama'ama. The western shore offers ulua, moi, and 'o'io fishing.

CHART 37





38/Kauai, Niihau, Kaula

The island of Kauai (Chart 38), about 63 miles west-northwest of Oahu, is the oldest, most weathered, and most verdant of the larger islands. This beautiful "Garden Isle" abounds in rivers and cascading waterfalls. The island consists mainly of a single mountain, Waialeale (5,080 feet), with marginal lowlands except on the northwest. The chief scenic attractions are Waimea Canyon—the "Grand Canyon of the Pacific"; the spacious Hanalei Valley where rice and taro are cultivated on native-built terraces; and the Na Pali coast on the northwest with its 4,000-foot high precipices. Niihau, a small island southwest of Kauai, is privately owned and operated as a cattle ranch. Kaula Island is uninhabited, and access is sometimes restricted by the military.

OFFSHORE AND NEARSHORE FISHING

Kauai has some of the finest year-round deep-sea fishing in Hawaiian waters and boasts some world-record-size 'ahi, 'o'io, and kamanu. Charters are available out of Nawiliwili Harbor, Hanalei, and Port Allen. At Hanalei you have a choice of either deep-sea or inshore bonefishing excursions.

Ledge fishing (trolling and bottomfishing) is excellent around these islands. The submarine ledges are productive bottomfishing areas for 'opakapaka, uku, and kahala, which are taken in water about 100 fathoms deep. Ono and small 'ahi (usually under 100 pounds) are plentiful year-

round from about 25 to 100 fathoms. The peak of ono fishing is September, October, and November, when huge schools of akule, upon which ono feed, move into the area. It is also the peak time for small 'ahi; both ono and 'ahi are taken by trolling.

Anglers troll for marlin and large 'ahi (over 100 pounds) in deeper waters from about 100 to 1,000 fathoms. Tremendous schools of 'ahi move into Kauai waters in the late spring, with sizes known to reach a world record of 276 pounds. Marlin are fished year-round, but most fishing is in summer (May to September) when aku, the prime bait for marlin, move into the area in large schools. From September to January, aku are still present around the island, but are not as tightly schooled.

Mahimahi, although caught in Kauai waters, are not as abundant here as around the islands located farther east.

SHORE FISHING

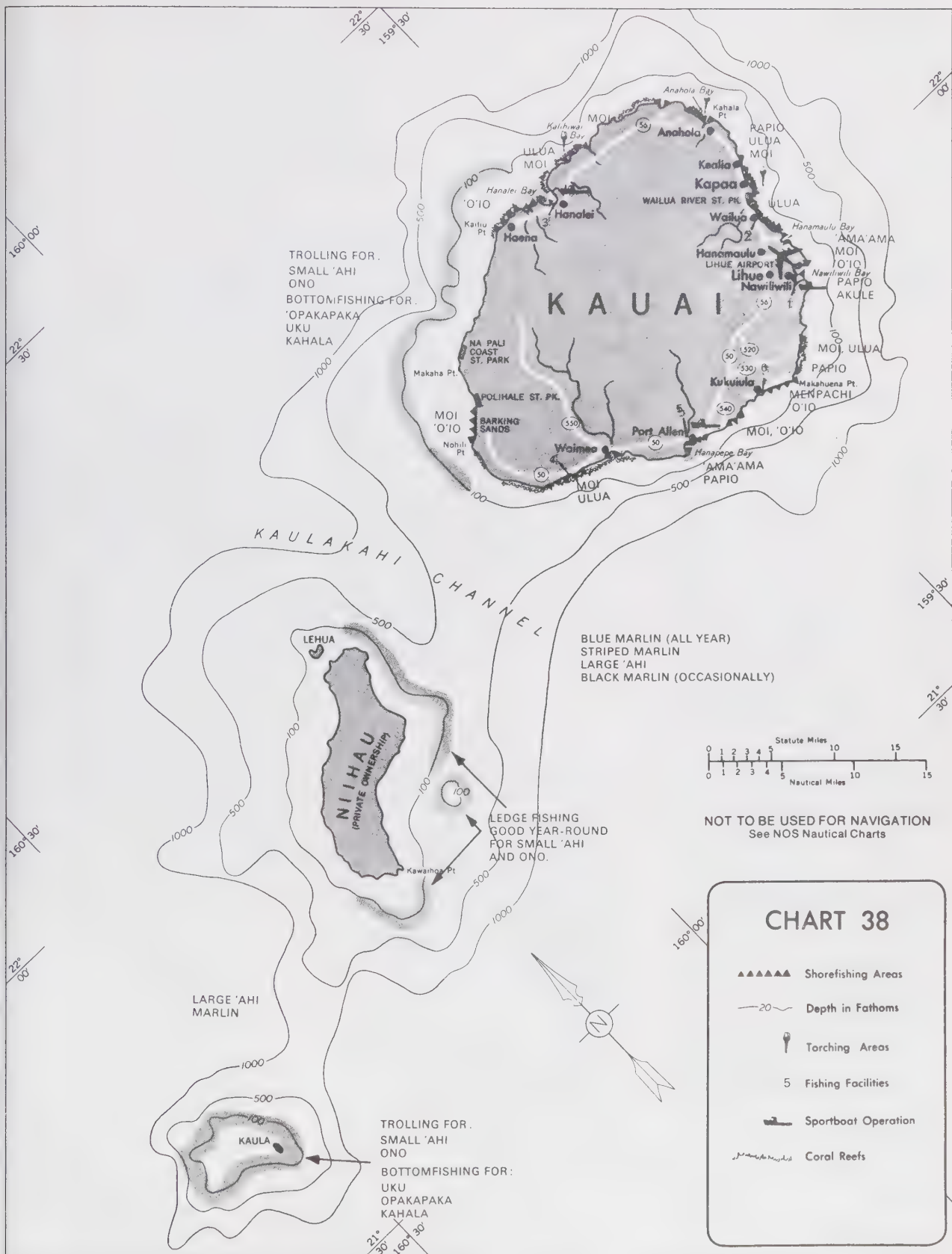
'O'io, papio, moi, and 'ama'ama are abundant all around the island of Kauai. 'Aweoweo, menpachi, hahalalu, and various kinds of goatfish are taken by shore anglers. Torch fishing and "squidding" are popular, especially in Kapaa Bay, Anahola Bay, and over the reef off Haena. At Haena during moonlit nights at low tide, the local people enjoy reef fishing with bamboo poles for 'upapalu or "moonlight fish." There is pier fishing for a variety of

fishes at Nawiliwili Harbor, Hanalei, Port Allen, and Kukuuiula Harbor.

One of the finest bonefishing grounds in the world is located off Hanalei along the north shore, where the former world record was held for years (18 pounds 2 ounces). Hawaiian bonefish ('o'io) are taken surf fishing or bottomfishing with cut bait—water conditions are not conducive to fly fishing.

FACILITY NUMBER
SPORT BOAT OPERATION
PIER FISHING
SKIFF RENTALS
LAUNCHING
JETTY FISHING
LOCATION

- | | | |
|---|-----------|-----------------------|
| 1 | ● ● ● ● ● | Nawiliwili Harbor |
| 2 | ● ● | Wailua Marina |
| 3 | ● ● ● ● ● | Hanalei |
| 4 | ● ● ● ● ● | Kikiaola Boat Harbor |
| 5 | ● ● ● ● ● | Port Allen |
| 6 | ● ● ● ● ● | Kukuuiula Boat Harbor |





39/AMERICAN SAMOA

The tropical islands of American Samoa (Chart 39) are in the south Central Pacific Ocean, approximately 2,200 miles southwest of the Hawaiian Islands and 1,600 miles northeast of the northern tip of New Zealand. American Samoa is an Unincorporated Territory of the United States and comprises seven islands—Tutuila, Aunu'u, Ta'u, Olosega, Ofu, Swains, and Rose Atoll. Five of these islands are mountainous and volcanic in origin, and two (Rose Atoll and Swains Island) are tiny coral atolls each less than 2 miles in diameter. The combined land area of all the islands is a scant 76.2 square miles, or about one-sixteenth the land area of our smallest State, Rhode Island.

The five larger islands are surrounded intermittently with narrow stretches of coral reef, beyond which the water depth plunges fairly rapidly away from shore. Submerged bank areas may extend out $\frac{1}{2}$ to 4 miles before dropping dramatically from 50 fathoms to depths greater than 500 fathoms. The islands are bathed by the warm waters of the South Equatorial Current system, with sea surface temperatures ranging from 75° to 86°F over the course of a year.

The climate of American Samoa is tropical, and air temperatures are fairly uniform, averaging 78° to 80°F at sea level. Rainfall is generally heavy, increases with altitude, and is greater on the south and east coasts. Trade winds blow from the southeast quarter about 80% of the time but are relatively light compared to those of Hawaii. Best weather is from November to April when these winds are generally lightest.

About 90% of the total population of 27,000 is located on Tutuila Island, the largest of the island group and where Pago Pago is located. The island is about 18 miles long and 5 miles wide

with a mountain range along its length. It is nearly bisected by the deep waters of Pago Pago Harbor, one of the finest and most beautiful ports in the South Pacific.

A tourist industry is developing rapidly on Tutuila Island, and the increased tourism has brought a growing interest in the sport fishing potential of Samoa's productive grounds which now yield high commercial catches of billfish and tuna. Two licensed sport fishing boats are now available for charter out of Fagatogo on Pago Pago Bay. Fishing grounds are close in and offshore of the island.

OFFSHORE FISHING

Large game fish are abundant throughout the year in Samoan waters, and many good fishing locations are within a relatively short run from port. Billfish grounds off Tutuila Island produce saula (blue marlin), saula-lele (sailfish), asi (yellowfin tuna), atu (skipjack tuna), rainbow runner, masimasi (dolphin), and ono (wahoo). Waters on the north side of the islands are virtually unfished, but show potential of being excellent big game fishing grounds as well. While they are caught year-round, the best time for large asi is March to July, and for atu, October to March.

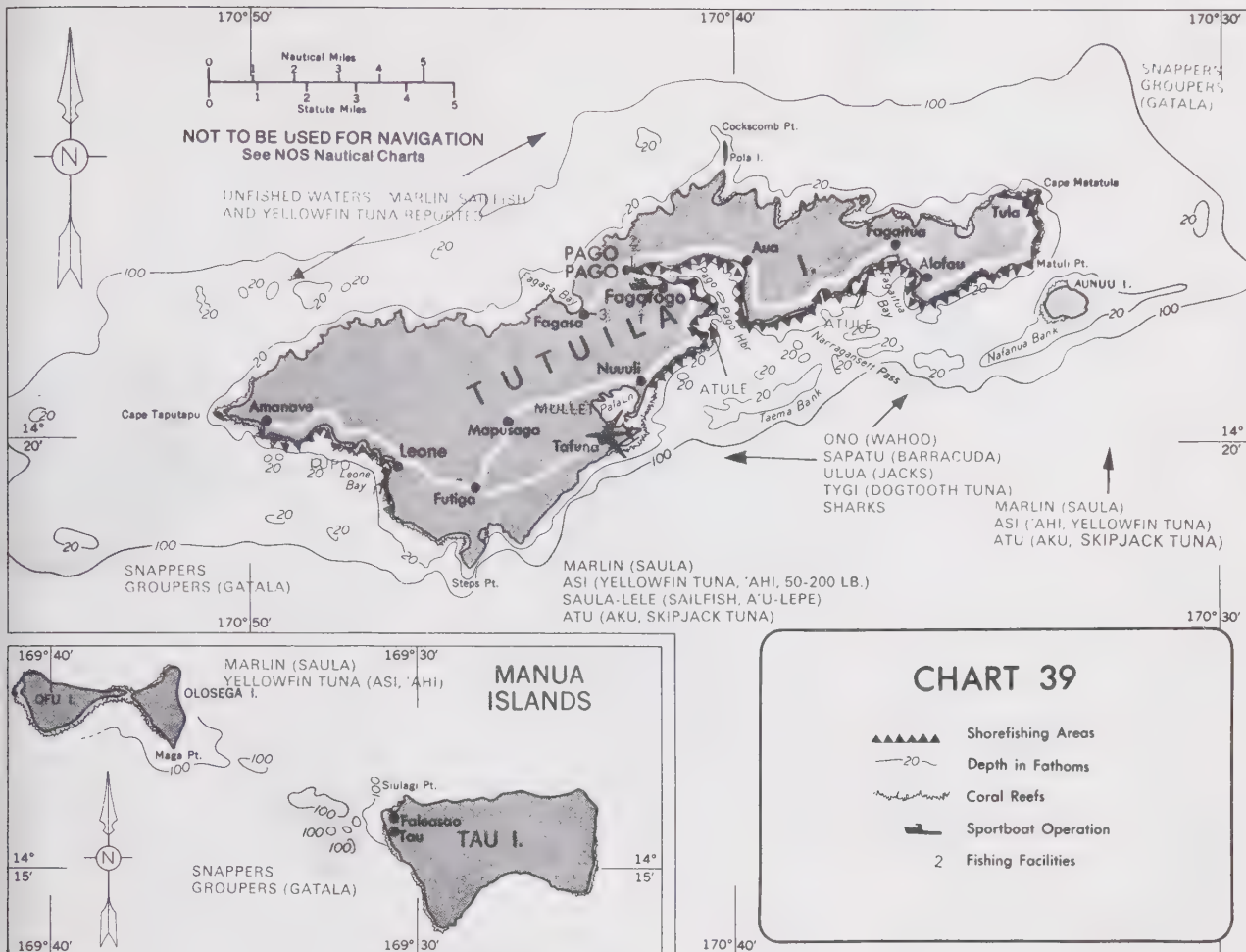
Inshore of the billfish grounds along the 100-fathom drop off, there is handlining and trolling for ono, tagi (dogtooth tuna), sapatu (barracuda), and large jacks or ulua. Most tagi are caught handlining at dusk or at night. Sharks are also common along these ledge areas, particularly the gray reef shark.

Bottomfishing is excellent and usually takes place in waters 100 fathoms or less; the main catch consists of groupers and snappers. Visitors to the island should be warned that the flesh of some snappers may be

toxic, and it is wise to inquire locally about the edibility of certain species. Groupers, collectively called "gatala" by Samoans, are generally taken at 10 to 40 fathoms over reefs and ledge areas. The most common species are gatala, gatala moana, i'a manaia, and ata'ata, which is similar to California's giant sea bass and ranges up to 500 pounds but generally is from 100 to 400 pounds. Of the snappers, the most common varieties are the colorful bluelined snapper or savani, which is the most abundant; the green snapper or filoa (reported to be slightly toxic in Samoan waters); and the red snapper or mala'i. Another common snapper caught handlining, known locally as mu, is definitely known to cause ciguatera poisoning and should not be eaten. Aso'ama, (uku), a nontoxic snapper, is sometimes taken over bottomfishing areas along with some of the large jacks, atule (akule), sapatu, tagi, and sharks. Deepwater snappers such as opakapaka and palu (onaga) are more abundant farther offshore over ledges at 200 to 300 fathoms. These deeper areas, however, are

FACILITY NUMBER
SPORT BOAT OPERATION
PIER FISHING
SKIFF RENTALS
LAUNCHING
JETTY FISHING
LOCATION

- 1 ● ● ● ● Fagatogo
- 2 ● ● Pago Pago
- 3 ● ● Fagasa



seldom fished because fishing for other game fishes is so good closer to Tutuila Harbor. The same is true for the bottomfishing areas around the Manua Island group, which are fished mainly by natives who launch canoes in the surf on the west end of Ta'u Island. Rose Atoll, a turtle and bird preserve, is also too far from port to be a feasible fishing ground at this time.

SHORE FISHING

The inshore reefs of Tutuila abound with over 600 varieties of colorful fishes, and few have gone untasted by the Samoans, who prefer to comb nearby reefs rather than venture to offshore fishing grounds. As a result, these reefs have been subjected to heavy fishing pressure over the years and, unfortunately, are showing signs of depletion.

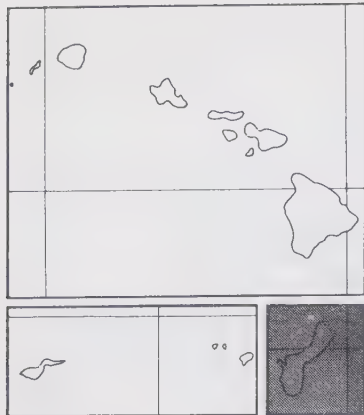
Most shore fishing is done by wading out over the reefs at high tide. A variety of sea creatures are captured in an almost equal variety of

ways—with traps, nets, spears, hook and line, or simply bare hands and a pail. The most common methods are bamboo pole fishing and cast netting. Young snappers and groupers are the main catch, but "lupo" (young jacks), "malau" and other squirrelfishes, goatfishes, and even an occasional butterflyfish and surgeonfish are taken. The shore is accessible all along the southern side of the island and on the north shore at Fagasa where the road follows the shoreline. It is advisable to check with local chiefs or matai before fishing near their villages—just as you would ask a property owner permission before fishing on his land. Spearing is legal, but generally discouraged.

Atule and mullet are fished in lagoons and bays around the island. Atule are caught in good numbers by pole fishing from shore in Pago Pago Harbor, mainly from the docks and piers on the west side of the harbor. Unlike his Hawaiian counterpart, the Samoan atule is caught easily during the day as well as at night. Skiff

anglers also catch this tasty little fish handlining. Mullet are taken in sandy bays and lagoons with cast nets, and Palu Lagoon is considered one of the best fishing areas for this silvery schooling fish.

A very unusual fishery exists in American Samoa, one which the population looks forward to with eager anticipation. It is the fishery for palolo. Each year at a predictable time in either October or November, the tail ends of a species of reef-dwelling sea worm become detached and swim to the surface in wriggling masses. The tail sections are full of eggs and sperm which are discharged into the water. On these nights, and usually only for a few hours, the reef comes alive with great swarms of palolo. The natives, armed with dip nets, pails, and other capturing devices, wade out over the reefs to scoop up large quantities of this unusual Samoan delicacy. Palolo are usually eaten raw, but for the less brave they can be cooked with chopped onions or scrambled with eggs.



40/GUAM

Guam (Chart 40), about 3,340 miles west of Honolulu and 1,500 miles east of Manila, is the largest and southernmost island in the Marianas island group. Administered by the U.S. Navy for over half a century, the territory was placed under the administrative jurisdiction of the Department of the Interior in 1950 by executive order of the President of the United States. That year, the Organic Act was passed by the U.S. Congress and became Guam's Constitution, giving Guamanians U.S. citizenship and establishing the present 21-seat legislature.

The island is important as a distribution center for Micronesia and as a major link between these islands and the rest of the world. Because of its strategic geographical location and beautiful tropical setting, Guam has several large military bases, a growing tourist industry, and many thriving new businesses.

The physical geography of the island contrasts sharply north to south. The northern part of the island is a low-lying limestone plateau covered by a thick growth of jungle vegetation. The south, rising to more than 1,000 feet above sea level, is characterized by high volcanic hills covered with sword grass. The island is about 23 miles long and varies from 4 to 8 miles wide.

The climate is tropical with air temperatures ranging from 70° to 90°F. Daytime temperatures are usually in the mid-80's. Average rainfall is about 90 inches, three-quarters of which falls during the rainy season from July to October. The driest month is April.

Guam's offshore waters abound with a variety of game fish; undoubtedly the most famous is the Pacific blue marlin. On 21 August 1969, a world-record blue marlin was

caught off Ritidian Point near the northern tip of Guam. This huge fish weighed in at 1,153 pounds with a total length of 14 feet 8 inches. A fishing derby is held each year at the end of the Liberation Day celebration in July, and many sport anglers register for this annual event.

Most offshore fishing takes place on the leeward or western side of the island because of rough waters usually prevalent on the windward or eastern side. The trolling grounds produce blue marlin, black marlin, sailfish, yellowfin tuna, skipjack tuna, mahimahi, rainbow runner, tosun or wahoo, barracuda, and sharks. Marlin, wahoo, and tuna are caught occasionally throughout the year; the best time for mahimahi is during January and February; and yellowfin and skipjack tuna are usually most abundant February through August.

Bottomfishing is excellent over submarine ledge areas surrounding the island and over offshore banks. The catch consists mostly of snappers and groupers. Some of the more common snappers are the pink kali kali, pink paka, yellowtail, gendai, lehi, ehu, onaga or red, and tagafi. Groupers are collectively called "gadao" by Guamanians. Dogtooth tuna and jacks (called collectively tarakito) are also taken in some of the bottomfishing areas.

Many people on the island enjoy fishing from shore, and the most popular methods seem to be spin fishing and surround netting. The island is rimmed by many miles of beautiful coral reefs and the water over these reefs ranks among the clearest in the world, especially during the dry season. Anglers with spinning gear cast from the reef shelves for snappers, groupers, and jacks, and from the piers and in boat channels for atulai (akule or bigeye scad) and tataga (kala, unicornfish). Other fishes such as young snappers, wrasses, mullet, tarakitiyos (young jacks), needlefish, and achuman ('opelu or mackerel scad) are taken occasionally by hook-and-line anglers. The surround net captures an assortment of reef fishes including those mentioned above as well as some of the goatfishes and

parrotfishes. Cast net operators fling their circular nets over the water for fish that wander about the reefs in schools, such as manini (known locally as "kicho"), young mullet, goatfish, and sesjun (rabbitfish). There is also some spearing for octopus, parrotfish, and surgeonfish, as well as other reef fishes.

Some of the more popular shore-fishing areas are shown on the chart. Atulai are taken during most of the year (May to March) along the channel area that cuts through the reef at Agana and at the southern tip of the island near Merizo. There is shore fishing in Apra Harbor for papio, atulai, and occasionally achuman ('opelu). Tataga are taken at Agana and sometimes at the north side of Cabras Island, as well as near the reef's outer edge on the southern shore of Ylig Bay. The latter area also is good for snappers—mafuti, kakaka, and bua. It is advisable to check locally about the waters you plan to fish, since currents over the reefs are sometimes dangerous.

Sport fishing boats are available for charter out of Port Merizo and Agana. Skiffs can be rented at Port Merizo, and there are boat launching facilities at the Apra Harbor seaplane ramp and at the Agana boat basin.

FACILITY NUMBER
SPORT BOAT OPERATION
PIER FISHING
SKIFF RENTALS
LAUNCHING
JETTY FISHING
LOCATION

- | | | |
|---|-------|-------------------------|
| 1 | ● | Apra Hbr. seaplane ramp |
| 2 | ● ● | Agana Boat Basin |
| 3 | ● ● ● | Port Merizo |

CHART 40

 Shorefishing Areas

—20— Depth in Fathoms

Fishing Facilities

Sportboat Operation

Coral Reefs



NOT TO BE USED FOR NAVIGATION
See NOS Nautical Charts

145° 00'

MARLIN
YELLOWFIN TUNA ('AHI)
SKIPJACK TUNA (AKU)
TOSUN (ONO, WAHOO)

SNAPPERS TAKEN OCCASIONALLY
THROUGHOUT YEAR, WEATHER
PERMITTING :
PINK KALIKALI (KALIKALI)
PINK PAKA (OPAKAPAKA)
YELLOWTAIL KALIKALI

GADAO (GROUPER)
SNAPPERS
ONAGA
GINDAI

TOSUN (ONO, WAHOO)
YELLOWFIN TUNA ('AHI)
BARRACUDA
MARLIN
MAHIMAH

SNAPPERS 0
GINDAI
YELLOWTAIL KALIKALI

SNAPPERS
GINDAI

TARAKITO (JACKS)
TAKEN ALL YEAR,
WEATHER PERMITTING

YEAR ROUND, WEATHER PERMITTING

TARAKITO (JACKS)
ACHUMAN ('OPELU)
TAGAFI (MU)
GADAQ (GROUPERS)
SNAPPERS
LEHI
GINDAI

SNAPPERS
LEHI
YELLOW EYE PAKA
PINK PAKA ('OPAKAPAKA)
GINDAI
YELLOWTAIL KALIKALI

SKIPJACK TUNA (AKU)
TOSUN (ONO, WAHOO)
YELLOWFIN TUNA ('AHI)
MARLIN
MAHIMAHI

MAHMAHI EHU ('
MARLIN
TOSUN (ONO, WAHOO)
SKIPJACK TUNA (AKU)
YELLOWFIN TUNA ('AHI)

SNAPPERS:
GINDAI
SMALL LEH
YELLOWTAIL
KALIKALI

SNAPPERS:
ONAGA
LEHI
EHU ('ULA'U

ATATAGA
AATULAI (AKULE)

AGANA

TATAGA
(KALA)
SNAPPERS
MAFUTI
KAKAKA
BUA

BARRACUDA

(SEE INSET FOR
GALVEZ BANK AREA)

MARINE GAME FISHES

The following pages list some of the more common marine game fishes caught within the geographical areas covered in this Guide. Major species are illustrated. Fishes taken along the west coast of the continental United States are described first; those taken around the tropical Pacific islands of Hawaii, American Samoa, and Guam are covered on succeeding pages. The list is separated in this way to assist the reader in finding the fishes familiar to his general geographic area. To help avoid confusion with common fish names an index to common names referred to in this list is provided in the back of the guide. All-tackle records are those recognized by the International Game Fish Association as of 1974. Fish illustrations by Susan E. Smith.

Marine Game Fishes of the United States West Coast

This list describes those marine and anadromous species commonly taken by anglers along and off the coasts of California, Oregon, Washington, and Alaska.

Off southern California most pelagic species taken by the marine angler are subtropical, and common only from Point Conception south to off Baja California, Mexico. Point Conception, 40 miles west of Santa Barbara, Calif., is generally agreed to be the major ecological and faunal dividing point for many pelagic species. However, Pacific bonito, Pacific mackerel, and bluefin tuna, which are common in the south, occur at times north of Point Conception, and conversely, northern species such as coho salmon sometimes range south of Point Conception. In the deeper cooler water over the continental shelf are also found many species that range north of the Point.

From Point Conception north to south central Alaska one encounters a fairly constant species composition

throughout this temperate environment. North of Point Conception, extending to at least Cape Blanco, Oreg., there exists a major coastal "upwelling" area which results in cool water nearshore much of the year. Another environmental change from temperate to subarctic occurs from about the Aleutian chain in Alaska north beyond the Bering Sea.

For the most part, this list uses common and scientific names as defined in the American Fisheries Society checklist [Bailey et al. 1970], except for the use of "surfperch" for all members of the family Embiotocidae. Some species descriptions will have more than one common name; however, the common name approved by the American Fisheries Society is capitalized. The authorized scientific name and the name of the individual credited with describing the species for the scientific record are given last.

For those anglers wishing to ensure correct identification of their west coast catch, we suggest the

following publications. Much of the information in this list was derived from identification lists prepared by the following authors:

- Hart, J. L.
1973. Pacific fishes of Canada. Fish. Res. Board Can., Bull. 180, 740 p.
- Miller, D. J., and R. N. Lea.
1972. Guide to the coastal marine fishes of California. Calif. Dep. Fish Game, Fish Bull. 157, 235 p.
- Phillips, J. B.
1957. A review of the rockfishes of California (Family Scorpaenidae). Calif. Dep. Fish Game, Fish Bull. 104, 158 p.
- Tarp, F. H.
1952. Revision of the Family Embiotocidae (the surfperches). Calif. Dep. Fish Game, Fish Bull. 88, 99 p.

ALOPIIDAE: THRESHER SHARKS

1.



1. THRESHER SHARK, fox shark swiveltail, *Alopias vulpinus* (Bonnaterre). DISTRIBUTION: Temperate and tropical waters of the Pacific, Indian, and Atlantic oceans and the Mediterranean Sea. SIZE: Reported to reach 20 to 25 feet (610-762 cm) long and weigh up to 1,000 pounds (453.6 kg) or more. However, the usual catch is less than 30 pounds (13.6 kg). All-tackle record for the Pacific (Mayor Island, New Zealand) is 729 pounds (330.7 kg) and 101 inches (256.6 cm) long. COLOR: Gray to black above, fading to white below. □ A pelagic shark common to the offshore waters of the eastern Pacific south of Cape Flattery, Wash. Caught during summer in central and southern California; best fishing is in the Los Angeles outer harbor. One of the most desirable species of shark for table food, also excellent when smoked.

LAMNIDAE: MACKEREL SHARKS

2.



2. SHORTFIN MAKU, bonito shark, *Isurus paucus* Rafinesque. DISTRIBUTION: Temperate and tropical waters of the Pacific Ocean to Hawaii and Japan. Known in the eastern Pacific from the Columbia River to Chile. SIZE: Reported to reach 12 feet (366 cm) long and weigh up to 1,000 pounds (453.6 kg). However, the size usually ranges from 4 to 8 feet (122-244 cm) long. All-tackle record in the Pacific (Mayor Island, New Zealand) is 1,061 pounds (481.3 kg) and 12 feet 2 inches (370.9 cm) long. COLOR: Dark gray above, white below. □ Appears off the southern California coast in summer, and is the subject of a growing sport fishery. A pelagic shark, may be dangerous to humans, but regarded as a good food species.

CARCHARHINIDAE: REQUIEM SHARKS

3.



3. BLUE SHARK, *Prionace glauca* (Linnaeus). DISTRIBUTION: Tropical and temperate seas of the world; in eastern Pacific Ocean from Chile to the Gulf of Alaska. SIZE: Length is reported to 15 feet (457 cm), but most caught off southern California are less than 8 feet (244 cm) and weigh less than 50 pounds (22.7 kg). All-tackle record in the Atlantic (Rockport, Mass.) is 410 pounds (186.0 kg) and 11½ feet (350.6 cm) long. COLOR: Dark blue above, white below. □ One of the more important pelagic sharks in catches of the southern California sport fishery during summer and fall. Good fighter on light tackle, but not a particularly good food species. Common to offshore waters, but also occurs inshore off southern and central California during summer and fall.

4.



4. BROWN SMOOTHHOUND, *Mustelus henlei* (Gill). DISTRIBUTION: Gulf of California, Mexico, to Humboldt Bay,

Calif. SIZE: Reaches about 3 feet (91 cm) long. COLOR: Reddish brown fading to white on belly. □ Common in bays from San Francisco south and is one of the most abundant sharks entering the sport fishery catch. It is a good sport species on light tackle and frequently taken by anglers along sandy shores, from piers, and in harbors.

5. GRAY SMOOTHHOUND, *Mustelus californicus* Gill. DISTRIBUTION: Mazatlán, Mexico, to Cape Mendocino, Calif. SIZE: Length recorded to about 5 feet (152 cm). COLOR: Dark gray to brown above, white below. □ Of minor importance to sport anglers; commonly taken in the surf zone, however.



6. LEOPARD SHARK, cat shark, *Triakis semifasciata* Girard. DISTRIBUTION: Mazatlán, Mexico, to Oregon. SIZE: reported to attain 6½ feet (198 cm) in length. COLOR: Gray with black spots and crossbars; belly lighter. □ Abundant in central and southern California and caught largely in bays, off jetties, and along sandy beaches most of the year. Caught in large numbers during the fall in San Francisco Bay. A desirable food species.

RHINOBATIDAE: GUITARFISHES

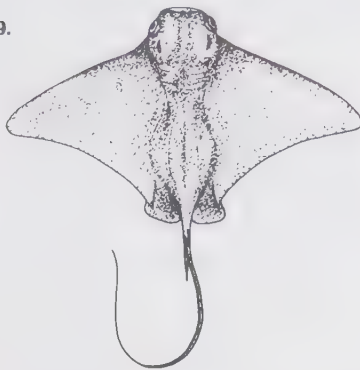


7. SHOVELNOSE GUITARFISH, shovelnose shark, *Rhinobatos productus* (Ayres). DISTRIBUTION: Gulf of California, Mexico, to Monterey Bay, Calif. SIZE: Reaches a length of about 5 feet (152 cm) and a weight of up to 40 pounds (18.1 kg). COLOR: Brownish gray, white underside. □ Often caught by pier, bay, and surf anglers, and common over sand and mud bottom in shallow bays and estuaries in southern California. Not a desirable food species, although the dorsal meat is reported to be palatable. Provides considerable recreation and taken all year throughout most of its range.

8. THORNBACK, *Platyrrhinoidis triseriata* (Jordan and Gilbert). DISTRIBUTION: Turtle Bay, Baja California, Mexico, to central California. Rare north of Point Conception. SIZE: Length to about 2½ feet (76 cm). COLOR: Brown on back, white or cream colored below. □ Although taken in fair numbers, they are not the major objective of most anglers. Common in depths less than 150 feet (45.7 m).

MYLIOBATIDAE: EAGLE RAYS

9.



9. BAT RAY, *Myliobatis californica* Gill. DISTRIBUTION: Gulf of California, Mexico, to Oregon. SIZE: Maximum known weight is about 210 pounds (95.3 kg) with a spread of 4 feet (122 cm). COLOR: Dark brown to black above, white below. □ Only member of the eagle ray family caught in California, where it occurs along the outer coast and is commonly taken in bays such as San Diego Bay, Newport Bay, Los Angeles Harbor, Morro Bay, San Francisco Bay, and Tomales Bay. The bat ray is an active fighter and is classed as a good game species. It has a venomous spine on dorsal side at base of tail that can cause painful wounds. General treatment is to cleanse the wound thoroughly and immerse in warm to hot water with baking soda. Consult doctor for relief from pain and possible secondary infection.

ACIPENSERIDAE: STURGEON

10.



10. WHITE STURGEON, Pacific sturgeon, *Acipenser transmontanus* Richardson. DISTRIBUTION: Ensenada, Baja California, Mexico, to Gulf of Alaska. SIZE: Largest white sturgeon taken along the Pacific was reported to be about 20 feet (610 cm) long weighing 1,800 pounds (816.5 kg). However, today it would be uncommon to catch one over 500 pounds (226.8 kg). COLOR: Uniform gray. □ An important species taken in Suisun, San Pablo, San Francisco, and Coos bays, the Columbia River estuary, upper Willapa Bay, and upper Grays Harbor. Heavy fishing in the late 1800's for caviar and smoked sturgeon reduced the population drastically. Today the lower Columbia River appears to be the center of distribution; in the San Francisco area the numbers of sturgeon appear to be increasing and the fishery is becoming more popular. Several species of sturgeons exist in North America. Some are found only in fresh water, and some, like the white sturgeon, are anadromous.

11. GREEN STURGEON, *Acipenser medirostris* Ayres. DISTRIBUTION: Ensenada, Baja California, Mexico, to Alaska, Bering Sea, and Japan. SIZE: Length to 7 feet (213 cm), weight to 350 pounds (158.8 kg); most caught are much smaller than this. COLOR: Olive green with three longitudinal olive stripes on body. □ Similar in habits to the white sturgeon, although less is known of its life history.

SALMONIDAE: TROUT AND SALMON

12.



12. CHINOOK SALMON, king, spring, tyee, Quinnot, *Oncorhynchus tshawytscha* (Walbaum). Young juveniles or "feeders" are sometimes called "blackmouth." DISTRIBUTION: Southern California to Alaska and south on the Asiatic side to the Amur River, USSR, also to northern Japan. SIZE: Record weight reported to 126½ pounds (57.4 kg); however, few are caught over 50 pounds (22.7 kg), and most average 18 to 25 pounds (8.2-11.3 kg) when mature. COLOR: At sea, dark gray above with silver sides and belly; black spots on back and both lobes of tail; gums at base of teeth black. □ Most desirable of marine game fish in northern waters and subject of an extensive ocean troll fishery. Principal fishing areas begin in the south off Pismo Beach and Avila, Calif., and extend into southern Alaska. Fished primarily by trolling with dead bait or lures, and drift fishing with live or frozen bait. Offshore fishing depth for this species is usually greater than for other salmon species.

13.



13. COHO SALMON, silver salmon, silversides, salmon trout, *Oncorhynchus kisutch* (Walbaum). DISTRIBUTION: Coronado Islands, Mexico, to Alaska, and south on the Asiatic side to Japan. SIZE: Coho grow to a length of 3 feet (91 cm) and a weight of 30 pounds (13.6 kg) or possibly more; most in the sport catch average less than 10 pounds (4.5 kg). COLOR: At sea, metallic blue green above; silver sides and belly; small black spots on back, dorsal fin, and upper lobe of tail fin; gums at base of teeth white. □ Ocean trolling for coho ("silvers") is most successful from near Fort Bragg, Calif., northward, although some are caught in the San Francisco area and a few are taken as far south as Point Mugu, Calif., area every year. Principal fisheries for this species are along the coasts of Oregon, Washington, and Alaska. Fishing technique used in the ocean is much the same as for other salmon.

14.



14. PINK SALMON, humpback salmon, *Oncorhynchus gorbuscha* (Walbaum). DISTRIBUTION: Southern California to northwestern Alaska and along the Asian coast. SIZE: Reported to reach 2½ feet (76 cm) long and a maximum weight of about 12 pounds (5.4 kg). Averages about 6 pounds (2.7 kg) when mature. COLOR: Metallic blue above; silvery on sides; oval spots on tail and back with many as large or larger than eye diameter. □ Smallest of the five species of salmon. Common to the west coast, but usually not common south of Oregon. Major fisheries for this species are in the Strait of Juan de Fuca, in Puget Sound, and to the north. Pink salmon usually do not run very far upstream; most spawn in the lower parts of rivers. They are unique among Pacific salmon in that all fish mature at the end of their second year. Larger runs are reported in odd-numbered years in Puget Sound area; in Alaska, runs occur in both odd- and even-numbered years, depending on specific area fished.

15.



15. SOCKEYE SALMON, red salmon, blueback salmon, *Oncorhynchus nerka* (Walbaum). DISTRIBUTION: Southern Oregon to northwestern Alaska and Asia. SIZE: Length reported up to 2½ feet (76 cm); weight up to about 5 to 7 pounds (2.3-3.2 kg). COLOR: Greenish blue above, with greenish head; silvery on sides. □ Best fishing is from northern Oregon to northwestern Alaska and Asia. Spawning season lasts from March to August; major season is from June to August. Usually enters rivers that are fed by lakes. The sockeye salmon rarely takes a hook so is not a major contributor to the sport catch.

16.



16. CHUM SALMON, dog salmon, fall salmon, *Oncorhynchus keta* (Walbaum). DISTRIBUTION: Southern California to northwestern Alaska and Asia. SIZE: Length up to 3½ feet (107 cm); average weight of 10 to 12 pounds (4.5-5.4 kg) when mature. COLOR: In brackish or salt water, fish are metallic blue above, sometimes with faint black specks; dark tips on pectoral, anal, and caudal fins. □ Best areas of fishing are from Washington north to off British Columbia, near the inshore areas along the Strait of Georgia. The chum salmon appears in late summer and fall in spawning schools, after spending usually about 3 to 5 years at sea.

17.



17. CUTTHROAT TROUT (sea-run), blueback, Columbia River trout, seatrout, *Salmo clarki* Richardson. DISTRIBUTION: Eel River, Calif., to southeastern Alaska, with some running into brackish and salt waters from coastal streams; rarely in the ocean off California. SIZE: Length reported up to 2½ feet (76 cm); weights usually run from 1 to 3 pounds (0.5-1.4 kg). COLOR: Greenish blue above; silvery on sides. Identified by a red slash under lower jaw; however, this may not be present in fish migrating from salt water. □ Best fishing found north of the Columbia River in brackish-water areas. Spawns February to May in small coastal streams, young sometimes descend in second or third year and usually remain in estuaries for 1 or more years before returning to spawn. A predator on young salmon in the spring.

18.



18. RAINBOW TROUT, steelhead, sea-run rainbow trout, seatrout, salmon trout, silversides, *Salmo gairdneri* Richardson. DISTRIBUTION: Northern Baja California, Mexico, to Alaska, Bering Sea, and Japan, with some running into salt water, though not now common south of Point Conception. SIZE: Reported to reach 3½ feet (107 cm) long and 36 pounds (16.3 kg) in weight; the usual catch is much smaller, averaging under 10 pounds (4.5 kg). COLOR: At sea, steel blue above, with silvery sides. □ Taken in the estuarine areas of both large and small streams, and also off river mouths. Season for fishing most coastal streams is December through March, usually best after winter rains result in a breakthrough of the "bar" at the mouth of the stream. In larger and cooler rivers, spawning run may start earlier in late summer or early fall. Some steelhead enter certain tributaries in spring or summer, and remain through the dry season until the following spring before spawning. This species spawns more than once; some may return to spawn for a second or third time.

19.

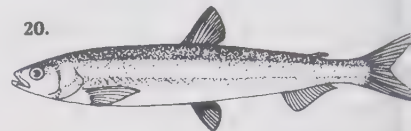


19. DOLLY VARDEN, Dolly, Oregon char, redspotted trout, salmon trout, malma trout, bull trout, seatrout, *Salvelinus malma* (Walbaum). DISTRIBUTION: Northern California to northwestern Alaska, running into saltwater estuarine areas. SIZE: Length reported to 3 feet (91 cm) and

maximum weight of 20 pounds (9.1 kg); usual catch is 1 to 3 pounds (0.5-1.4 kg) in weight and 15 to 20 inches (38-51 cm) long. COLOR: Olive green to brown above with pale-yellow spots; orange-red spots on sides. Sea-run fish are silvery. □ Common to Puget Sound and southeastern Alaska. In some streams there is a seaward migration in spring and an upstream spawning migration in fall.

OSMERIDAE: SMELTS

20.



20. SURF SMELT, day smelt, silver smelt, surfish, *Hypomesus pretiosus* (Girard). DISTRIBUTION: Long Beach, Calif., to Prince William Sound, Alaska. SIZE: Maximum length is about 10 inches (25 cm); average catch is about 8 inches (20 cm) or less. COLOR: Light olive green; sides silver with purple hue. □ Distinguished from the night smelt by its small mouth, which does not extend beyond a line drawn vertically from the middle of the eye. Best areas for fishing are north of Monterey Bay, Calif. Surf smelt does not spawn south of Scott Creek, Santa Cruz County, Calif. Shore spawning runs occur from March to September during daylight along sandy shores near river mouths. Surf smelt runs are correlated with the tides, and fish are usually caught with "A"-frame nets. In the north they are taken by jigging from piers, in late winter.

21.



21. NIGHT SMELT, surfish, *Spirinchus starksi* (Fisk). DISTRIBUTION: Point Arguello, Calif., to Shelikof Bay, Alaska. SIZE: Length reported to about 9 inches (23 cm); usual length of catch is about 5 to 6 inches (13-15 cm). COLOR: Sides silver; olive green on back. □ Similar in many respects to surf smelt, but the mouth is larger and extends to below the posterior edge of the eye. Common to sandy shores (coarse sand) from central California to coastal Washington. Night smelt does not spawn south of Moss Landing, Calif. It appears to concentrate in much the same areas as the surf or day smelt, but spawns during darkness, and runs are not adjusted to tides. Method of capture is similar to that used for the surf smelt.

22.



22. EULACHON, candlefish, hooligan, smelt, *Thaleichthys pacificus* (Richardson). DISTRIBUTION: Bodega Bay, Calif., to Bering Sea, Alaska. SIZE: Reported to attain a length of 12 inches (30 cm). COLOR: Uniform light bluish, brown

above; silvery on sides and belly. □ Common to the coasts of Oregon, Washington, and Alaska. Fished with nets about mouths of rivers and inlets as the fish migrate inshore to spawn in rivers from Mad River, Calif., northward to Alaska (March, April, and May). It is a very oily fish, and called candlefish because when dried and threaded with a wick it may be used as a candle.

SMELTS OF LESS IMPORTANCE TO THE MARINE ANGLER:

23. LONGFIN SMELT, *Spirinchus thaleichthys* (Ayres). DISTRIBUTION: San Francisco Bay, Calif., to Prince William Sound, Alaska. SIZE: To about 6 inches (15 cm). COLOR: Sides silver with brownish dorsal areas. □ Spawns in coastal rivers and composes a minor portion of the sport smelt catch.

24. WHITEBAIT SMELT, *Allosmerus elongatus* (Ayres). DISTRIBUTION: San Pedro, Calif., to Strait of Juan de Fuca. COLOR: Sides silver; back greenish. □ Similar in appearance to the night smelt, but like the longfin, it composes a minor portion of the total sport catch of smelt. Spawning behavior not known.

GADIDAE: CODFISHES



25. PACIFIC COD, true cod, *Gadus macrocephalus* Tilesius. DISTRIBUTION: Santa Monica, Calif., to northwestern Alaska and Asia (Yellow Sea). SIZE: Length recorded to at least 3½ feet (114 cm) and weight up to 40 pounds (18.1 kg). COLOR: Brownish gray above fading to lighter below; brown spots on upper parts; edges of fins white. □ An excellent food species commonly available off the coast of northern Oregon, Washington, and Alaska. Migrates from deep to shallower water, though usually caught in water deeper than 60 feet (18.3 m). Reported to spawn in winter and in early spring and is abundant in coastal waters at that time.



26. PACIFIC TOMCOD, *Microgadus proximus* (Girard). DISTRIBUTION: Point Sal, Calif., to Unalaska Island, Alaska. SIZE: Usually less than 12 inches (30 cm) long and 1 pound (0.5 kg) in weight; fish over 2 pounds (0.9 kg) are very rare. COLOR: Olive or brownish above; white on sides and belly. □ Abundant from San Francisco north and taken by pier, jetty, and skiff anglers. A good food species, but sometimes discarded because of its small size.

27.



27. PACIFIC HAKE, *Merluccius productus* (Ayres). DISTRIBUTION: Gulf of California, Mexico, to Alaska and Asiatic coast. SIZE: Record length to about 3 feet (91 cm); most are 1 to 1½ feet (30-46 cm) long. COLOR: Gray to dusky brown, with a brassy overtone. □ Sometimes taken off Oregon and Washington while salmon fishing in deep water. It is not a desirable sport species, though it is suitable for eating if prepared promptly.

ATHERINIDAE: SILVERSIDES

28.



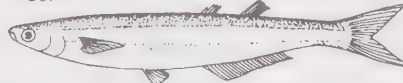
28. JACKSMELT, smelt, *Atherinopsis californiensis* Girard. DISTRIBUTION: Santa Maria Bay, Baja California, Mexico, to Yaquina Bay, Ore. SIZE: Reported to reach a length of 22 inches (56 cm); most fish caught weight about ½ pound (0.2 kg) or less. COLOR: Dusky green above, sides silvery; metallic band edged above with blue extends length of body. □ Commonly found year-round in bays and turbid-water areas. Usually caught in water of less than 100 feet (30.5 m). Known to spawn in bays during winter and spring, sometimes in sizable schools. One of the most abundant species in the catch of pier anglers in southern and central California.

29.



29. TOPSMELT, smelt, *Atherinops affinis* (Ayres). DISTRIBUTION: Gulf of California, Mexico, to Vancouver Island, British Columbia. SIZE: Length to about 14 inches (36 cm); average weight about ¼ pound (0.1 kg). COLOR: Bluish gray to bright green above, silvery below; metallic band edged above with blue or purple extends length of body. □ Frequents the same general areas and habitats as the jacksmelt. Fairly common in pier catches along the central California coast. Distinguished from the jacksmelt by placement of the first dorsal fin, which is located farther back, the last rays being opposite the origin of the anal fin.

30.

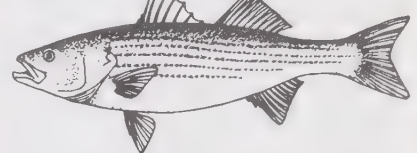


30. CALIFORNIA GRUNION, *Leuresthes tenuis* (Ayres). DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to San Francisco Bay, Calif. SIZE: Length to

about 7 inches (18 cm); average weight to about ¼ pound (0.1 kg) or less. COLOR: Bluish green above, silver below; a lateral metallic band tinged with blue and bordered above with violet extends length of body. □ A southern California fish, not common north of Point Conception. Tends to range along sandy shoreline, usually in water less than 50 feet (15.2 m) deep. Best beaches for catching grunion are from Los Angeles south to Mexico. Spawns from March through August. Beaches itself between waves to spawn at night during high tides following the first three to four nights after the full and the dark of the moon.

PERCICHTHYIDAE: TEMPERATE BASSES

31.



31. STRIPED BASS, striper, rock bass, *Morone saxatilis* (Walbaum). DISTRIBUTION: Descanso Point, Baja California, Mexico to Barkley Sound, British Columbia. SIZE: Reported up to 6 feet (183 cm) and 125 pounds (56.7 kg) in the Atlantic. All-tackle record (Cuttyhunk, Mass.) is 72 pounds (32.7 kg), with a length of 54½ inches (138 cm). In the Pacific, reported to reach about 4 feet (122 cm) and 90 pounds (40.8 kg); average catch is less than 10 pounds (4.5 kg). COLOR: Brownish green above; silvery on sides and belly; seven or eight lateral stripes. □ Best fishing areas are in San Francisco Bay and the Sacramento-San Joaquin River Delta area where it was introduced from the east coast in 1879. Other good fishing spots are found at Coos Bay, Ore., where a separate population has established itself. This species sometimes ranges south and north along the coast from San Francisco in summer during years of high sea surface temperatures, and is taken by surf anglers as far south as Monterey Bay (occasionally Morro Bay) and north to the Russian River. Migrates from bays and upper tidal areas into river systems to spawn, usually in April and May.

32.



32. GIANT SEA BASS, black sea bass, *Stereolepis gigas* Ayres. DISTRIBUTION: Gulf of California, Mexico, to Humboldt Bay, Calif. SIZE: Recorded up to over 500 pounds (226.8 kg) and over 7 feet (213 cm) long. All-tackle record for the Pacific (Anacapa Island, Calif.) is 568½ pounds (258.0 kg), with a length of 7 feet 5 inches (226.1 cm). Some live to a very old age; a 435-pound (197.3-kg) fish was determined to be between 72 and 75 years old. COLOR: Dark brown to gray with blackish

hue above becoming lighter below; juveniles have dark spots on sides. □ In recent years the population level of this species is much reduced in southern California. Best fishing is found about Anacapa Island and near kelp beds from La Jolla, Calif., south along Baja California, Mexico, and in the Gulf of California. Large fish prefer rocky bottom, just outside kelp beds and along drop offs in water 115 to 150 feet (35.1-45.7 m) deep. Small fish can be found over sandy areas around and in the kelp in shallower water of about 40 to 70 feet (12.2-21.3 m) deep.

SERRANIDAE: SEA BASSES

33.



33. KELP BASS, calico bass, bull bass, *Paralabrax clathratus* (Girard). DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to Columbia River. SIZE: Greatest weight recorded is 14½ pounds (6.6 kg) and a length to 28 inches (71 cm). They are reported to attain an age of 20 years or more. COLOR: Olive or brownish above with sides mottled with angular lighter shaded areas, becoming silvery below; belly and fins tinged with yellow. □ Common from Point Conception, Calif., to Baja California, Mexico, in coastal kelp beds. A major game species about kelp beds in southern California and a good food fish. Nonmigratory, spawning April through the fall in and near kelp over rough bottom. Distinguished from the barred sand bass in that the third, fourth, and fifth dorsal spines are about the same length, whereas the third dorsal spine of the barred sand bass is much longer than the other spines.

34.



34. SPOTTED SAND BASS, *Paralabrax maculatofasciatus* (Steindachner). DISTRIBUTION: Gulf of California and Mazatlán, Mexico, to Monterey Bay, Calif. SIZE: Length to about 22 inches (56 cm). COLOR: Greenish to olive brown above, becoming white below, with black spots on body and fins. □ A sandy-shore and near-offshore species in southern California. Commonly caught in bays and around harbor entrances.

35.



35. BARRED SAND BASS, sand bass, sugar bass, ground bass, *Paralabrax nebulifer* (Girard). DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to Santa Cruz, Calif. SIZE: Length to about 25½ inches (65 cm). COLOR: Dark gray to greenish brown on back, with vertical irregular dusky bands; paler below; golden-brown spots on cheeks and snout. □ Distinguished from the kelp bass by the long third dorsal spine. Commonly caught over nearshore sandy bottom flats, in bays, and near kelp beds and rocky areas in southern California. Best catches are during summer.

BRANCHIOSTEGIDAE: TILEFISHES

36.



36. OCEAN WHITEFISH, whiting, blanquillo, *Caulolatilus princeps* (Jenyns). DISTRIBUTION: Peru to Vancouver Island, British Columbia. SIZE: Weights recorded up to 12 pounds (5.4 kg); however, 3 to 5 pounds (1.4-2.3 kg) is normal. COLOR: Rich brown to yellowish on back becoming lighter below with light spots on sides; yellow edging on fins; dorsal and anal fins with blue stripe; pectoral bluish with yellow stripe. □ Frequently caught from Point Conception, Calif., south to off Mexico. Usual depths of fishing are from 30 to 300 feet (9.1-91.4 m) over rocky bottom. Good fishing around southern California islands and offshore banks such as Cortez and Tanner banks. Best fishing is spring through fall.

CARANGIDAE: JACKS AND POM-PANOS

37.



37. YELLOWTAIL, juarel, white salmon, amberjack, *Seriola dorsalis* (Gill). DISTRIBUTION: Chile to southern Washington. SIZE: Usual weight about 10 to 20 pounds (4.5-9.1 kg); record fish in the California-Mexico area reported to about 5 feet (152 cm) long weighing 80 pounds (36.3 kg). All-tackle record for the Pacific (Bay of Islands, New Zealand) is 111 pounds (50.3 kg) and 62 inches (157.5 cm) long. COLOR: Bright metallic blue to brownish green above, yellow lateral stripe from eye to

yellow tail; white below. □ A major sport species in southern California, frequently taken at the Coronado Islands and off Baja California, Mexico, as well as around Catalina Island and around kelp beds off San Diego north along the coast to the Santa Barbara Channel Islands. It is a migratory pelagic species, occurring during summer and early fall in southern California.

38.



38. JACK MACKEREL, Spanish mackerel, horse mackerel, saurel, *Trachurus symmetricus* (Ayres). DISTRIBUTION: Baja California, Mexico, to southeastern Alaska, and offshore out to 500 miles. SIZE: Length usually to about 1 foot (30 cm); reported to 32 inches (81 cm). COLOR: Iridescent bluish green, mottled on back becoming lighter on sides and fading to silvery below. □ A major commercial species and an important sport fish in southern California. Frequently taken from sport boats and sometimes from jetties and piers in southern California. In its northern range it is sometimes taken from piers. Best fishing is July through September.

CORYPHAENIDAE: DOLPHINS

39.



MALE



FEMALE

39. DOLPHIN, mahimahi, dorado, *Coryphaena hippurus* Linnaeus. DISTRIBUTION: Tropical and temperate seas. Recorded off the west coast from Chile north to off Grays Harbor, Wash. SIZE: All-tackle record for the Atlantic (Spanish Wells, Bahama Islands) is 85 pounds (38.6 kg) and 69 inches long (175.3 cm). In the Pacific, weight reported to 45 pounds (20.4 kg) and length to 6 feet (183 cm). COLOR: Brilliant blue or blue green above; sides bright golden yellow spotted with bright blue and white-green spots; white below. When dying, this fish will flash many rapidly changing colors. □ During some years having warmer water they are taken in fair numbers while surface trolling for striped marlin off San Diego, Calif. A brilliantly colored fish and an excellent fighter.

POMADASYIDAE: GRUNTS

40.



40. SARGO, china croaker, *Anisotremus davidsoni* (Steindachner). DISTRIBUTION: Gulf of California, Mexico, to Santa Cruz, Calif., rare north of Point Conception, Calif. SIZE: Reported to attain 23 inches (58 cm) and 4 pounds (1.8 kg); however, most angler-caught sargo are much smaller than this. COLOR: Silver with grayish tinge on back; edge of gill cover black; dark spot on base of fin; vertical bar extending down from middorsal fin area. □ Found nearshore and in bays, common to shallow waters with rocky bottom, or about piers. Best fishing during summer.

SCIAENIDAE: DRUMS

41.



41. WHITE SEABASS, Catalina salmon, seatrout, croaker, *Cynoscion nobilis* (Ayres). DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to Juneau, Alaska. SIZE: Length to 5 feet 5½ inches (166.4 cm) and weight of 83¾ pounds (38.0 kg)—an all-tackle record for a fish caught near San Felipe, Mexico. Average catch is 5 to 25 pounds (2.3-11.3 kg). COLOR: Steel blue to gray above with gold highlights, silvery below. Young have several dark vertical bars. □ A prized game fish and excellent food species. Caught along the coast northward from Baja California, Mexico, to central California. Most are caught near the mainland shore over sandy bottom or around the edges of kelp beds; also near the kelp beds about Catalina and San Clemente islands. Young white seabass are commonly taken close to shore in southern California.

42.



42. YELLOWFIN CROAKER, Catalina croaker, *Umbrina roncadore* Jordan and Gilbert. DISTRIBUTION: Gulf of California, Mexico, to Point Conception, Calif. SIZE: Length recorded to about 18 inches (46 cm) and up to 3 pounds (1.4 kg). COLOR: Gray to iridescent blue, sometimes metallic green with a brassy luster above, shading to silvery white below; wavy lines on sides

deep olive; fins mostly yellow. □ Usually caught in shallow water over sandy bottom in the surf zone, and in bays and sloughs. It is a migratory species, and best fishing is in late summer, especially at Newport Beach and San Onofre, Calif.

43.



43. CALIFORNIA CORBINA, corvina, California whiting, surf-fish, *Menticirrhus undulatus* (Girard). DISTRIBUTION: Gulf of California, Mexico, to Point Conception, Calif. SIZE: Reaches a length of about 2½ feet (76 cm) or more and is reported to reach a weight of 8 pounds (3.6 kg). COLOR: Gray to steel blue with silvery luster on back, paling to white below; sometimes has a wavy diagonal line on sides. □ The corbina is a surf-zone species common from Point Conception south along sandy shores. The area from Long Beach (Belmont Shores) to San Diego is reported to have the best fishing. Corbina are found inshore during summer and are believed to range into deeper water during winter. Best fishing is July to October. An excellent food species.

44.



44. SPOTFIN CROAKER, golden croaker, *Roncadore stearnsi* (Steindachner). DISTRIBUTION: Mazatlan, Mexico, to Point Conception, Calif. SIZE: Reported to reach a length of at least 27 inches (69 cm) and a weight of 10½ pounds (4.8 kg). COLOR: Silver gray with bluish luster above, becoming white below; dark spot at base of pectoral fin. □ This species is common south of the San Pedro-Long Beach, Calif., area and is fished along sandy beaches and in bays. Known to congregate in "holes" outside the surf zone. Spawns offshore in summer and tends to be a coastal migratory species. Late summer is best time for fishing.

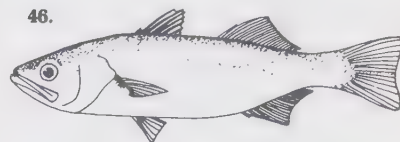
45.



45. WHITE CROAKER, kingfish, tomcod, roncky, *Genyonemus lineatus* (Ayres). DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to Vancouver Island, British Columbia. SIZE: Average weight of angler catch is usually less than 1 pound (0.5 kg). Largest recorded size was 15½ inches (39 cm) and about 1½ pounds (0.7

kg). COLOR: Silver with a brownish brassy luster above, becoming lighter below; fins yellowish (except pelvics). □ Abundant in shallow bays and lagoons from San Francisco, Calif., south. Also taken in and just outside the surf zone over sandy bottom, usually at depths of 10 to 60 feet (3.0-18.3 m); seldom caught at depths over 200 feet (61.0 m). Good food fish though small in size.

46.



46. QUEENFISH, herring, *Seriphus politus* Ayres. DISTRIBUTION: Off Magdalena Bay, Baja California, Mexico, to Yaquina Bay, Oreg. Rare north of Monterey, Calif. SIZE: Reaches a length of 1 foot (30 cm). COLOR: Bluish above, silvery below; fins yellowish. □ Known to occur in schools in shallow-water areas over sandy bottom. Common in bays and sloughs. Not a particularly desirable sport species; however, it provides considerable recreation to the southern California angler.

47. BLACK CROAKER, black bass, blue bass, china croaker, *Cheilotrema saturnum* (Girard). DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to Point Conception, Calif. SIZE: Length to about 15 inches (38 cm). COLOR: Adults are bluish or dusky black with a coppery sheen above; silver below with dark specks; gill cover edged with black; pelvic fins black. □ Somewhat rare and taken only irregularly by southern California anglers.

KYPHOSIDAE: SEA CHUBS

48.



48. HALFMOON, Catalina perch, blue perch, *Medialuna californiensis* (Steindachner). DISTRIBUTION: Gulf of California, Mexico to Klamath River, Calif. SIZE: Maximum recorded length is 19 inches (48 cm) with a weight to near 5 pounds (2.3 kg), although the usual catch is much smaller in size. COLOR: Slate colored to dark blue above, becoming paler blue and mottled on sides and below. □ A popular fish with the rocky shore angler. Best fishing is along the coast of southern California and about its offshore islands. Common to rocky shores and kelp beds. Best depths for fishing are from near the surface to 100 feet (30.5 m).

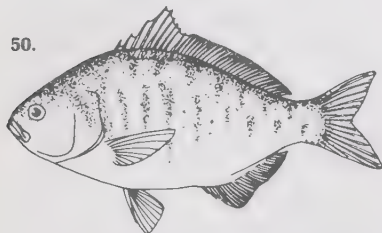
49.



49. OPALEYE, blue-eye perch, black perch, button perch, Catalina perch, blue bass, blacksmith, *Girella nigricans* (Ayres). DISTRIBUTION: Cape San Lucas, Baja California, Mexico, to San Francisco, Calif. SIZE: Record size reported to be about 25¼ inches (64 cm) and weight to 13½ pounds (6.1 kg); average size is less than 4 pounds (1.8 kg). COLOR: Greenish blue to olive above, becoming paler below; eye opalescent blue green; young with one or two white spots on back at base of dorsal fin. □ Best fishing areas are south of Point Conception, Calif., near rocky areas located near kelp beds. Common from the surface to about 60 to 100 feet (18.3-30.5 m) below the surface. Spawns during April, May, and June.

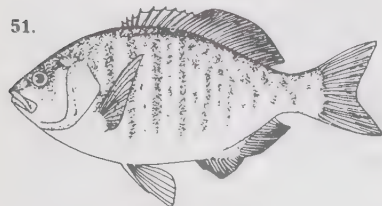
EMBIOTOCIDAE: SURFPERCHES

50.



50. REDTAIL SURFPERCH, porgy, *Amphistichus rhodotus* (Agassiz). DISTRIBUTION: Monterey Bay, Calif., to Vancouver Island, British Columbia. SIZE: Length reported up to 16 inches (41 cm). COLOR: Light olive green above, silver sides and belly; orange to brassy bars alternating across lateral line; light red to purple caudal, anal, and pelvic fins. □ Primarily a sandy-shore species, abundant in the surf zone from northern California northward. Best catches around the mouths of streams and during spring. Sometimes taken from piers and jetties near inlets.

51.



51. BARRED SURFPERCH, *Amphistichus argenteus* Agassiz. DISTRIBUTION: Playa Maria Bay, Baja California, Mexico, to Bodega Bay, Calif. SIZE: Usual size caught by the angler is 1 to 2 pounds (0.5-0.9 kg) with a record catch of 17 inches (43 cm) and 4½ pounds (2.0 kg). COLOR: Olive green to yellow green on back, silvery below; vertical bars on sides with intermittent spots. □ The major surf species

in southern California; most abundant along the coast from Morro Bay, Calif., south into Mexico. A very important game fish in the sandy surf zone where it congregates in bottom depressions. Shore fishing is best from December to March.

52.



52. CALICO SURFPERCH, *Amphistichus koelzi* (Hubbs). DISTRIBUTION: Northern Baja California, Mexico, to Shi Shi Beach, Wash. SIZE: Average weight is near 1 pound (0.5 kg); maximum recorded length is over 11 inches (28 cm). COLOR: Light olive above, fading to silver below; brownish specks forming irregular crossbars; sometimes brassy luster on head and belly. □ Common in central California from Morro Bay to the San Francisco area. Beaches in the Monterey Bay area are reported to offer excellent fishing for this species. Caught in the sandy surf zone and frequently appears in the pier catch.

53.



53. WALLEYE SURFPERCH, *Hyperprosopon argenteum* Gibbons. DISTRIBUTION: Point San Rosarito, Baja California, Mexico, to Vancouver Island, British Columbia. SIZE: Usual length is from 4 to 6 inches (10-15 cm) with a record length of about 12 inches (30 cm). Average weight is a little over ¼ pound (0.1 kg). COLOR: Metallic gray above fading to silver on sides and belly; dusky bars sometimes present on sides; usually identified by its large eyes and black-tipped pelvic fins. □ Found mostly over sandy bottom near rocky areas. Probably the most abundant surfperch common to the open rocky coast and in bays. A shallow-water species and a dominant one in pier catches.

54.



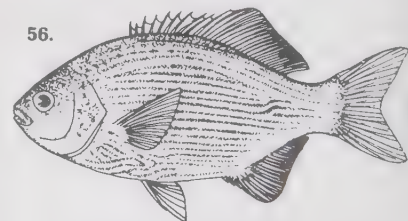
54. SILVER SURFPERCH, silver perch, *Hyperprosopon ellipticum* (Gibbons). DISTRIBUTION: Rio San Vicente, Baja California, Mexico, to Vancouver Island, British Columbia. SIZE: Reaches a maximum length of about 10½ inches (27 cm). Most catches are much smaller and average weight is about one-tenth of 1 pound (0.05 kg). COLOR: Metallic dark gray above, silver on sides and belly; dusky bars on sides; tail usually pink. □ This small surfperch is another sandy-shore species taken by surf anglers. Similar in appearance to the walleye surfperch; however, it does not have black-tipped pelvic fins.

55.



55. BLACK SURFPERCH, black perch, *Embiotoca jacksoni* Agassiz. DISTRIBUTION: Point Abreojos, Baja California, Mexico, to Fort Bragg, Calif. SIZE: Usual weight about ¾ pound (0.3 kg); known to reach a length of 15¼ inches (39 cm). COLOR: Variable, dark olive green to light reddish brown sometimes tinged with red or yellow; occasionally with blue stripes formed by small blue crescents in the middle of each scale; anal and pelvic fins often reddish orange. □ Common to rocky coasts near kelp areas; also found around piers, pilings, and in coastal bays. A shallow-water species, only rarely taken in sandy surf.

56.



56. STRIPED SURFPERCH, *Embiotoca lateralis* Agassiz. DISTRIBUTION: Point Cabras, Baja California, Mexico, to Port Wrangel, Alaska. SIZE: Average weight little over 1 pound (0.5 kg); maximum length recorded 15 inches (38 cm). COLOR: Red, blue, and yellow stripes along scale rows over coppery background on body; head with blue spots and stripes; pelvic fins dusky. □ This colorful surfperch is commonly caught around rocky shores, near pilings, or bulkheads in bays; frequently

found in kelp bed areas. An important sport species along the northern California, Oregon, Washington, and British Columbia coasts.



57. RUBBERLIP SURFPERCH, *Rhacochilus toxotes* Agassiz. DISTRIBUTION: Turtle Bay, Baja California, Mexico, to Russian Gulch, Calif. SIZE: Length recorded to 18½ inches (47 cm). COLOR: Variable, often brown to dusky blue above, shading to tanish silver on belly, fins dark except for pectorals, which are often pale orange or yellow; lips are a distinctive light pink. □ An excellent food species, and one of the more desirable of the surfperches. Central and southern California are the best fishing areas. Found near rocky areas and in bays around pilings or other underwater structures.

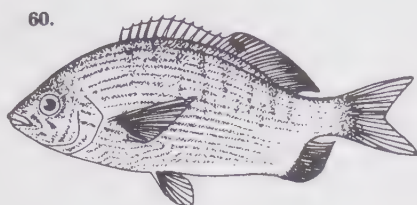


58. PILE SURFPERCH, *Damalichthys vacca* (Girard). DISTRIBUTION: Guadalupe Island, Baja California, Mexico, to Port Wrangel, Alaska. SIZE: Average weight is about 1¼ pounds (0.6 kg); maximum recorded length is slightly over 17 inches (43 cm). COLOR: Variable, from brown to gray black above, silvery to dusky on sides; dark vertical bar on midbody; fins dusky tipped. □ This species is common, as its name indicates, to pilings, piers, and other shallow-water obstructions in coastal bays. Sometimes it is taken from kelp areas and near rocky shores. Best fishing areas are found north of Point Conception to Vancouver Island, British Columbia.



59. WHITE SURFPERCH, *Phanerodon furcatus* Girard. DISTRIBUTION: Point Cabras, Baja California, Mexico, to Vancouver Island, British Columbia. SIZE: Length up to 1 foot (30 cm); average weight about ½ pound (0.2 kg). COLOR: Silvery with dusky speckling on back, sometimes with a rosy-orange luster; fins yellowish white with dusky edge on tail fin; black line along base of soft dorsal fin. □ Common to

central and southern California and is usually caught from piers in bays, or off jetties at harbor entrances, generally over sandy bottom.



60. RAINBOW SURFPERCH, *Hypsurus caryi* (Agassiz). DISTRIBUTION: Santo Tomas, Baja California, Mexico, to Cape Mendocino, Calif. SIZE: Average weight about ½ pound (0.2 kg); known to reach a length of 16 inches (41 cm). COLOR: Vivid horizontal stripes of red, orange, and blue on sides; irregular streaks of sky blue and orange on head; pelvic fins bright blue and red orange. □ Found in rocky areas along the open coast and in bays in California. Few are caught south of the Los Angeles area. Similar to black perch in that they are rarely caught in sandy surf areas.



61. SHINER SURFPERCH, yellow shiner, *Cymatogaster aggregata* Gibbons. DISTRIBUTION: San Quintin Bay, Baja California, Mexico to Port Wrangel, Alaska. SIZE: Usually less than 4 inches (10 cm) long. Maximum weight about ½ pound (0.2 kg); length about 8 inches (20 cm). COLOR: Dusky back with sides and belly silver; three vertical yellow bars below lateral line. □ Abundant and one of the most easily caught surfperch. Ranges from nearshore to depths of over 200 feet (61 m); more common to shallow inshore areas around piers and pilings and near eel grass sloughs.

SURFPERCHES OF LESS IMPORTANCE TO THE MARINE ANGLER:

62. KELP SURFPERCH, *Brachyistius frenatus* Gill. DISTRIBUTION: Turtle Bay, Baja California, Mexico, to Vancouver Island, British Columbia. SIZE: Length about 8½ inches (22 cm). COLOR: Golden brown to reddish brown on back, becoming copper red below; fins light red. □ A minor game species, found off rocky coasts in kelp beds.

63. SPOTFIN SURFPERCH, *Hyperprosopon anale* Agassiz. DISTRIBUTION: Blanca Bay, Baja California, Mexico, to Seal Rock, Oregon. SIZE: Length to 6 inches (15 cm). COLOR: Body silver with dusky color on back; two large black spots on dorsal and anal fins. □ Taken occasionally by anglers, but generally of minor importance.

64. SHARPNOSE SURFPERCH, *Phanerodon atripes* (Jordan and Gilbert). DISTRIBUTION: San Benito Island, Baja California, Mexico, to Bodega Bay, Calif. SIZE: Length to 12½ inches (32 cm). COLOR: Silvery with dusky speckling on back; thin black line at base of soft dorsal fin; pelvic fins white. □ Similar in appearance to the white surfperch.

65. PINK SURFPERCH, *Zalembeius rosaceus* (Jordan and Gilbert). DISTRIBUTION: San Cristobal Bay, Baja California, Mexico, to central California. SIZE: Length is reported to be to 8 inches (20 cm). COLOR: Distinguished by its rosy-red coloration; pink brown on upper body; two brown spots under the dorsal fin. □ A deepwater species (30-300 feet or 9.1-91.4 m).

LABRIDAE: WRASSES



66. CALIFORNIA SHEEPHEAD, redfish, humpy, fathead, *Pisces pulchrum* (Ayres). DISTRIBUTION: Gulf of California, Mexico, to Monterey Bay, Calif.; uncommon north of Point Conception, Calif. SIZE: Length to about 3 feet (91 cm) and weight up to 36¼ pounds (16.4 kg). COLOR: Adult males have a black head and tail and a red band on the midsection; chin is white on both sexes. Adult females are dull red or brownish red. □ Best fishing is in coastal kelp beds and about the offshore islands south of Point Conception at depths of 50 to 100 feet (15.2-30.5 m). A fatty hump develops on the male's forehead during breeding season.

WRASSES OF LESS IMPORTANCE TO THE MARINE ANGLER:

67. ROCK WRASSE, *Halichoeres semicinctus* (Ayres). DISTRIBUTION: Gulf of California, Mexico, to Point Conception, Calif. SIZE: Length reported up to 5 inches (13 cm). COLOR: Greenish brown; dusky vertical bars; male with dark-blue bar under pectoral fin. □ Found over rocky bottom, but is of minor importance to sport anglers, if not undesirable, due to its habit of snatching bait from the hook.

68. SEÑORITA, *Oxyjulis californica* (Günther). DISTRIBUTION: Central Baja California, Mexico, to central California. SIZE: Length to 10 inches (25 cm). COLOR: Reddish orange above, yellow below; black area on caudal fin base. □ A long slender wrasse, very

abundant within its range, but like the rock wrasse, is considered a pest because it often steals bait intended for more desirable species.

SPHYRAENIDAE: BARRACUDAS

69.



69. PACIFIC BARRACUDA, California barracuda, scooter, barry, *Sphyræna argentea* Girard. DISTRIBUTION: Cape San Lucas, Baja California, Mexico, to Kodiak Island, Alaska; however, it is not common north of Point Conception, Calif. SIZE: Record weight is reported to be about 18 pounds (8.2 kg), and a length of about 4 feet (122 cm). COLOR: Grayish black with a blue tinge on back, and silvery or white on sides and belly; tail yellowish. □ A major game species in southern California, and sometimes caught farther north off Avila, Calif., in summer. Usually caught by trolling or casting live bait near the mainland coast or about the southern California islands. Summer is the best fishing season. Young fish are usually found closer to shore than the adults.

STICHAEDIDAE: PRICKLEBACKS

70.



70. MONKEYFACE PRICKLEBACK, monkeyface eel, blenny eel, *Cebidichthys violaceus* (Girard). DISTRIBUTION: San Quintin Bay, Baja California, Mexico, to Crescent City, Calif. SIZE: Length to 30 inches (76 cm). COLOR: Uniform dull black, sometimes with reddish spots on sides; two dark bars below eye. □ Common in rocky intertidal areas out to 80 feet (24.4 m), inhabiting deep rocky pools between the tide lines in crevices or holes in the rocks. Algae seems to be its primary food, although it also will take shrimp and other marine invertebrates. Most are caught by poke-polers—anglers who poke a baited hook into tide-pool crevices during low tide.

SCOMBRIDAE: MACKERELS AND TUNAS

71.



71. ALBACORE, longfin tuna, *Thunnus alalunga* (Bonnaterre). DISTRIBUTION: Temperate waters of the Atlantic Ocean; in the Pacific Ocean, from Gualalupe Island, Baja California, Mexico, to southeast

Alaska. SIZE: Reported to reach a length of 5 feet (152 cm) and a weight of 93 pounds (42.2 kg). A record sport-caught fish off California coast was reported to weigh 66¼ pounds (30.0 kg). All-tackle record for a fish caught off Cape Point, South Africa, weighed 70 pounds (31.8 kg) with a length of 50½ inches (128.3 cm). COLOR: Dark steel blue or gray blue on back becoming silver gray on sides and belly; narrow-white border on caudal fin. □ Best sport fishing is July through September (August best) offshore in southern California. Some sport anglers fish for albacore off central and northern California and Oregon in August and September. Albacore is a migratory pelagic species that tends to inhabit the clearer offshore California Current waters that lie outside the greenish-colored nearshore coastal waters.

72.



72. YELLOWFIN TUNA, Allison tuna, *Thunnus albacares* (Bonnaterre). DISTRIBUTION: Cosmopolitan in tropical and subtropical seas, Hawaiian Islands, eastern Pacific from Chile to Point Buchon, Calif. SIZE: Reported to 450 pounds (204.1 kg); however, catches are rarely over 125 pounds (56.7 kg). All-tackle record in the Pacific (San Benedicto Island, Mexico) is 308 pounds (139.7 kg), with a length of 84 inches (213.4 cm). COLOR: Dark metallic blue above, fading into silver gray below; iridescent yellow band running from head to tail. Fins lengthen with age and are tinged with yellow. Irregular white dots form bars on belly of younger fish. □ This species rarely enters the sport fishery off southern California in the summer, and then only during years having very high sea surface temperatures. Although not often caught off southern California, it is much sought after by U.S. anglers off the coast of Mexico.

73.



73. BLUEFIN TUNA, *Thunnus thynnus orientalis* (Temminck and Schlegel). DISTRIBUTION: In the eastern Pacific from Peru to Shelikof Straits, Alaska, and west to Asia (Kuril Islands). SIZE: Recorded weight to 297 pounds (134.7 kg) in Pacific; however, most angler-caught bluefin are in the range of 10 to 40 pounds (4.5-18.1 kg). COLOR: Deep blue above, silvery on sides and white below; irregular white spots on belly. □ Excellent game species, sometimes taken off southern California in summer, though not in great numbers. A pelagic schooling species, with popular fishing areas off Santa Monica Bay and Oceanside, Calif., and about Catalina, San Clemente, and the Coronado islands.

74.



74. PACIFIC BONITO, bonehead, *Sarda chiliensis lineolata* (Girard). DISTRIBUTION: Baja California to Gulf of Alaska. SIZE: Reported to reach a weight of 25 pounds (11.3 kg) and a length of 40 inches (102 cm); however, the usual weight of sport-caught bonito is 1 to 4 pounds (1.8 kg and under). COLOR: Metallic blue green to violet on back, fading to silver on sides and below; dark oblique stripes on back. □ A pelagic migratory schooling species commonly caught by trolling and live bait casting off southern California during summer and fall. Trolling is best off kelp beds and along the coast from Point Dume to La Jolla, Calif., and about Catalina, San Clemente, and the Coronado islands. Successful fishing depends on higher sea temperatures off southern California.

75.



75. CHUB MACKEREL, Pacific mackerel, zebra, greenback, striped mackerel, *Scomber japonicus* Houttuyn. DISTRIBUTION: Chile to the Gulf of Alaska and transpacific. SIZE: Average size of fish caught by anglers is about 1 pound (0.5 kg). The record length is reported to be 25 inches (64 cm) and a weight of near 6½ pounds (2.9 kg). COLOR: Dark green to blue above with dark wavy bars on back, shading into iridescent silvery on sides. □ A pelagic schooling species commonly caught near the coast off southern California. Fishing is good all year when abundant; however, the Pacific mackerel resource is now at a low level and catches are reduced. Best fishing is in summer and fall.

XIPHIIDAE: SWORDFISHES

76.



76. SWORDFISH, broadbill, *Xiphias gladius* Linnaeus. DISTRIBUTION: Worldwide in warm seas; from Chile to Oregon in the eastern Pacific. SIZE: The weight of most swordfish caught off southern California by anglers is within the range of 150 to 300 pounds (68.1-136.1 kg). All-tackle record in the Pacific (Iquique, Chile) is 1,182 pounds (536.2 kg) with a length of 14 feet 11 inches (454.8 cm). COLOR: Dark gray above, fading to silver gray or gray yellow on belly. □ In southern California, this excellent food fish is harpooned commercially and taken by

sport anglers during summer into fall by hook and line. It is usually associated with islands and banks, mouths of undersea canyons, and steep submarine ridges. Swordfishing is becoming a popular sport off southern California.

ISTIOPHORIDAE: BILLFISHES



77. **STRIPED MARLIN**, *Tetrapturus audax* (Philippi). **DISTRIBUTION**: Throughout the warmer waters of the Indian and Pacific oceans. In the eastern Pacific from Chile to Point Conception, Calif. **SIZE**: Known to reach a weight of 350 pounds (158.8 kg) and a length of 12 feet (366 cm). Average weight of fish caught off San Diego is 110 to 140 pounds (49.9-63.5 kg). All-tackle record in the Pacific (Cape Brett, New Zealand) is 394 pounds (178.7 kg) with a length of 134 inches (340.4 cm). **COLOR**: Dark purplish blue above, fading to silvery below; dorsal and anal fin cobalt blue; sides with light-blue stripes. □ This species is pelagic in habitat and is found throughout the tropical and subtropical Pacific. This is the major billfish species caught off southern California during summer and fall (mid-August to mid-September usually best). Caught by trolling baits or lures.

STROMATEIDAE: BUTTERFISHES

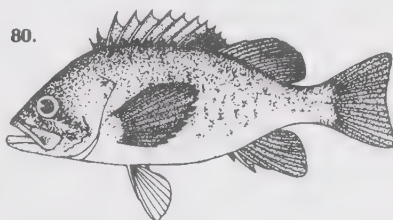


78. **PACIFIC POMPAÑO**, butterfish, *Peprilus simillimus* (Ayres). **DISTRIBUTION**: Magdalena Bay, Baja California, Mexico, to the mouth of Fraser River, British Columbia. **SIZE**: Length to about 11 inches (28 cm). **COLOR**: Iridescent silver green on back, becoming silvery on sides and belly. □ Commonly caught off southern and central California throughout the year. Usually found over sandy bottom. Frequently caught in bays during late summer and fall, offshore in deeper water for the rest of the year. An excellent food species.

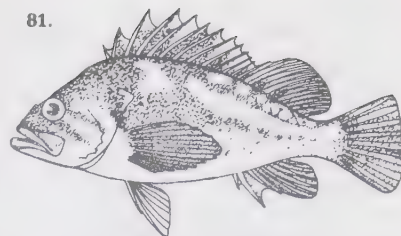
SCORPAENIDAE: SCORPIONFISHES



79. **BLUE ROCKFISH**, priestfish, bluefish, blue perch, *Sebastes mystinus* (Jordan and Gilbert). **DISTRIBUTION**: Point Santo Tomas, Baja California, Mexico, to Bering Sea, Alaska. **SIZE**: Record length is near 21 inches (53 cm); most catches are less than 15 inches (38 cm). **COLOR**: Dark blue above, shading to lighter below with light-blue mottling; fins uniformly blackish. Young are reddish up to 2½ inches (6 cm) long. □ Often confused with black rockfish, but distinguished by the slanted or straight anal fin, and absence of spots on dorsal fin. A shallow-water species usually found around rocky or kelp areas; however, they do range in depth to 200 or 300 feet (61.0-91.4 m). Best fishing from central California ports such as Morro Bay and Monterey Bay and north to off Oregon and Washington.



80. **BLACK ROCKFISH**, black snapper, black bass, bass rockfish, nero, cherna, *Sebastes melanops* Girard. **DISTRIBUTION**: Paradise Cove, Calif., to Amchitka Island, Alaska. **SIZE**: Usual weight of adults ranges to about 3 pounds (1.4 kg) and length is reported up to 23¾ inches (60 cm). **COLOR**: Black with gray mottling on sides shading to a white belly; black spots above the base of the spiny dorsal fin; fins dark gray. □ Often confused with the blue rockfish, but distinguished from it by the large mouth, rounded anal fin, and spots on dorsal fin. This species is abundant off northern California and Oregon, frequenting shallow-water reefs and commonly caught around kelp beds. It is sometimes taken by salmon trolling over deep offshore rocky areas.



81. **COPPER ROCKFISH**, *Sebastes caurinus* Richardson. **DISTRIBUTION**: Monterey, Calif., to Kenai Peninsula, Alaska. **SIZE**: Record length reported to be about 22½ inches (57 cm). Average weight is about 2½ pounds (1.1 kg). **COLOR**: Dark olive or brown back with darker mottlings, all over a coppery-brown tinge with a pale stripe along lateral line of rear two-thirds of body. Very similar to the whitebelly rockfish, *Sebastes vexillaris*, which differs slightly in coloration and has a more southerly range (San Benito Islands, Baja California, north to Crescent City, Calif.). □ Young inhabit shallow water, adults deeper water. Common off the coast of northern California, Oregon, and Washington to the Strait of Georgia, British Columbia.



82. **OLIVE ROCKFISH**, kelp yellowtail, kelp salmon, bass rockfish, sugar bass, *Sebastes serranoides* (Eigenmann and Eigenmann). **DISTRIBUTION**: San Benito Islands, Baja California, Mexico, to Redding Rock, Calif. **SIZE**: Reported to reach a length of 24 inches (61 cm); usual length is 6 to 12 inches (15-30 cm) and weight is usually less than 2 pounds (0.9 kg). **COLOR**: Olive brown above, fading to lighter on belly; whitish blotches on back under dorsal fin. □ Common to shallow water (50-100 feet or 15.2-30.5 m) around kelp beds and rocky bottom areas. Good fishing from central California south. Best fishing is along the southern California coast and about the offshore islands. Often confused with the yellowtail rockfish and kelp bass; however, if the number of soft rays in the anal fin is nine (instead of six to eight) it is very probably an olive rockfish. See also kelp bass for differences in dorsal fin shape.



83. **KELP ROCKFISH**, gopher rockfish, garrupa, *Sebastes atrovirens* (Jordan and Gilbert). **DISTRIBUTION**: Point San Pablo, Baja California, Mexico, to Timber Cove, Calif. **SIZE**: Usual weight is about 1 pound

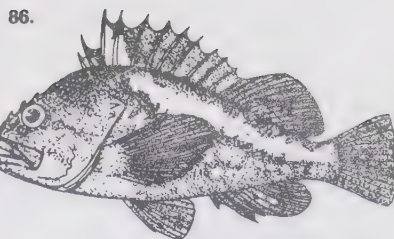
(0.5 kg); maximum length is reported to be near 17 inches (43 cm). COLOR: Mottled olive brown over lighter shades; throat yellow; head and body covered with dark speckles. □ As its name implies, this species is common around kelp beds and also found around rocky reefs. Younger fish are usually caught farther inshore in shallower water than the adults. Distinguished from the grass rockfish by the long gill rakers which are long and slender, not short and stubby as those of the grass rockfish.



84. GRASS ROCKFISH, kelp rockfish, scomoda, *Sebastes rastrelliger* (Jordan and Gilbert). DISTRIBUTION: Playa Maria Bay, Baja California, Mexico, to Yaquina Bay, Oreg. SIZE: Weight is usually less than 2 pounds (0.9 kg), with a record length reported to be about 22 inches (56 cm). COLOR: Dark green with light-green mottling above with lighter green or brown below; fins olive green with pelvic and pectoral fins tipped with red. □ Sometimes confused with the kelp rockfish. (See kelp rockfish for distinguishing characters.) This species is taken along the coast in shallow waters with best fishing off central California southward along the coast. Commonly caught in waters of 100 feet (30.5 m) or less, over or near kelp beds or rocky areas. The young are frequently caught from piers.



85. YELLOWTAIL ROCKFISH, green snapper, giolo, gialoto, cherne, yellowtail, *Sebastes flavidus* (Ayres). DISTRIBUTION: San Diego, Calif., to Kodiak Island, Alaska. SIZE: Average weight about 1½ to 2 pounds (0.7-0.9 kg); length reported to 26 inches (66 cm). COLOR: Mottled grayish brown above shading to white on belly; fins dusky yellow with tail fin tipped with bright yellow; tips of lower pectoral fin tinged with pink. □ Distinguished from olive rockfish by the eight soft rays in anal fin, and by presence of fine reddish-brown speckling on scales—olive rockfish almost always have nine soft anal rays and no speckling on sides. An important game fish species off the central California coast and to the north. Inhabits predominantly deepwater reefs.



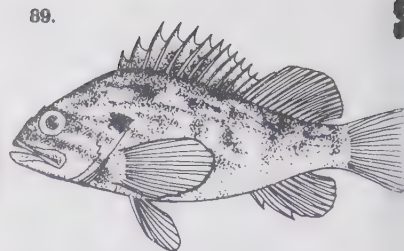
86. CHINA ROCKFISH, cefalutano, gopher, *Sebastes nebulosus* Ayres. DISTRIBUTION: San Miguel Island, Calif., north to southeastern Alaska. SIZE: Average weight about 2 pounds (0.9 kg); record length to 17 inches (43 cm). COLOR: Broad, bright yellowish stripe from dorsal fin area along lateral line on each side of blue-black body, with white spotting. □ Occurs nearshore and in water depths of 120 feet (36.6 m) or less. Caught over rocky bottom, sometimes in association with gopher, kelp, and grass rockfishes.



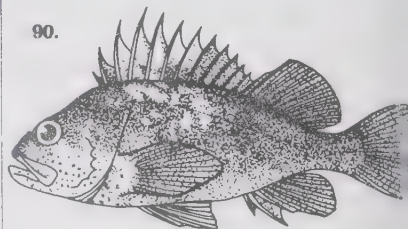
87. CALICO ROCKFISH, *Sebastes dalli* (Eigenmann and Beeson). DISTRIBUTION: Viscaïno Bay, Baja California, Mexico, to San Francisco, Calif. SIZE: Usually small. Average weight 1¼ pounds (0.6 kg); maximum length 8 to 10 inches (20-25 cm). COLOR: Greenish yellow with irregular brown bars and blotches on sides forming oblique bars; brown spots and streaks on tail fin. □ Common to southern California, with some taken off central California. Occurs in water 60 to 840 feet (18.3-256.0 m) deep. This species, however, does not appear to be greatly abundant in any one area.



88. WIDOW ROCKFISH, viuva, *Sebastes entomelas* (Jordan and Gilbert). DISTRIBUTION: Todos Santos Bay, Baja California, Mexico, to Kodiak Island, Alaska. SIZE: Average weight is about 1½ pounds (0.7 kg), and record length is 21 inches (53 cm). COLOR: Uniform dusky brown with a yellow or brassy tinge on sides and sometimes reddish on belly. Young specimens have vague orange streaks. □ Usually taken from below 100 feet (30.5 m) over rocky or rough bottom; however, young are caught near surface. This is an important species in the Monterey Bay area.



89. BROWN ROCKFISH, bolina, *Sebastes auriculatus* Girard. DISTRIBUTION: Central Baja California, Mexico, to southeastern Alaska. SIZE: Length to 21 inches (53 cm). COLOR: Brown with light brown mottling; dusky pink on fins and lower part of head; dark brown blotch on gill cover. □ Common around wharf piling and rocky areas in shallow water out to about 180 feet (54.9 m) from central California north, and fairly abundant in San Francisco Bay and Puget Sound.



90. QUILLBACK ROCKFISH, orange-spotted rockfish, yellow-backed rockfish, brown rockfish, speckled rockfish, *Sebastes maliger* (Jordan and Gilbert). DISTRIBUTION: Point Sur, Calif., to Gulf of Alaska. SIZE: Length to 24 inches (61 cm). COLOR: Slate brown with yellow mottling on back and on dorsal fin; orange spotting on ventral surface. □ Common in the northern part of its range where it tends to frequent inlets and shallow-water rockpiles. Fairly abundant in Puget Sound.

BROWN ROCKFISHES OF LESS IMPORTANCE TO THE MARINE ANGLER:

91. SILVERGRAY ROCKFISH, *Sebastes brevispinis* (Bean). DISTRIBUTION: Santa Barbara, Calif., to Bering Sea. SIZE: Length to 28 inches (71 cm). COLOR: Dark gray above, silver gray on sides and white below; fins pinkish.

92. DUSKY ROCKFISH, *Sebastes ciliatus* (Tilesius). DISTRIBUTION: Gualapup Island, Baja California, Mexico, to Point Conception, Calif. SIZE: Length to 11 inches (41 cm). COLOR: Gray brown with brown spots on dorsal area, becoming light gray below; brown streaks radiating from eye; fins pinkish.

93. GOPHER ROCKFISH, flesh-colored rockfish, *Sebastes carnatus* (Jordan and Gilbert). DISTRIBUTION: San Roque, Baja California, Mexico to Eureka, Calif. SIZE: Length to about 15½ inches (39 cm). COLOR: Olive brown with flesh-colored or whitish spotting and blotches.

94. **SQUARESPOT ROCKFISH**, smallmouth rockfish, *Sebastes hopkinsi* (Cramer). **DISTRIBUTION:** Guadalupe Island, Baja California, Mexico, to Farallon Islands, Calif. **SIZE:** Length to 11¼ inches (29 cm). **COLOR:** Yellow brown with dark brown blotches.

RED ROCKFISHES:



95. **VERMILION ROCKFISH**, red snapper, rasher, borracho, barrachon, red rock cod, genuine red, *Sebastes miniatus* (Jordan and Gilbert). **DISTRIBUTION:** San Benito Island, Baja California, Mexico, to Vancouver Island, British Columbia. **SIZE:** Record length to 30 inches (76 cm); weight reported to 15 pounds (6.8 kg). **COLOR:** Deep vermilion on back mottled with gray or blackish blotches on sides; orange stripes radiating from eye; fins deep red and on small specimens often faintly edged with black; mouth red. □ Sometimes confused with the canary rockfish; however, the underside of jaw is rough, not smooth, and there is no large black area on spinous dorsal fin as on smaller specimens of the canary rockfish. One of the larger rockfish species, common to depths of 200 to 600 feet (61.0-182.9 m). The young fish are frequently found near shore. An important contributor to the "rock cod" catch in southern California.



96. **CHILIPEPPER**, johnnies, johnny cod, *Sebastes goodei* (Eigenmann and Eigenmann). **DISTRIBUTION:** Magdalena Bay, Baja California, Mexico, to Vancouver Island, British Columbia. **SIZE:** Average weight is about 2¼ pounds (1.1 kg); maximum length is 22 inches (56 cm). **COLOR:** Reddish brown to copper above, shading to pink or white below with a distinct red stripe along the lateral line; fins pink. □ Fishing for this species is best off central and southern California. A deepwater species, it prefers rocky or mud bottom.



97. **BOCACCIO**, salmon grouper, young are sometimes called "tomcod," *Sebastes paucispinis* Ayres. **DISTRIBUTION:** Point Blanca, Baja California, Mexico, to Kodiak Island, Alaska. **SIZE:** Average weight is 3¼ pounds (1.5 kg); the record size reported to be about 3 feet (91 cm) and 21 pounds (9.5 kg). **COLOR:** Brownish to dusky red above, shading into dull orange red on sides, light pink on belly. Reddish tinge overall; sometimes mottled with brown or black. □ Usually distinguished from other rockfishes by its greatly projecting lower jaw. A very important commercial and sport species off California. Adults are fished in deep water (to 125 fathoms or 228.6 m), and young bocaccio are frequently found in schools nearshore and are commonly caught by pier anglers.



98. **CANARY ROCKFISH**, orange rockfish, codalargo, yellow snapper, filione, fantail, red rock cod, red snapper, *Sebastes pinniger* (Gill). **DISTRIBUTION:** Cape Colnett, Baja California, Mexico, to southeastern Alaska. **SIZE:** Average weight about 1½ pounds (0.7 kg) and a record length to about 30 inches (76 cm). **COLOR:** Grayish, mottled with orange; fins orange. Sometimes confused with vermilion rockfish. (See description of that species for differences.) □ Young canary rockfish are sometimes found in shallow water; adults found over banks in deep water. An important contributor to the central and northern California party boat catch.

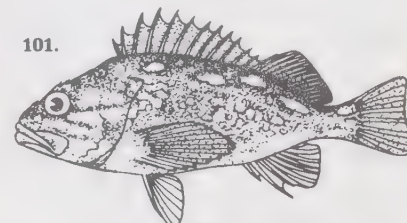


99. **YELLOWEYE ROCKFISH**, turkey-red rockfish, rashead rockfish, red snapper, red rockfish, tambor, turkey rock, potbelly, *Sebastes ruberrimus* (Cramer). **DISTRIBUTION:** Ensenada, Baja California, Mexico, north to Gulf of Alaska. **SIZE:** Average weight about 5½ pounds (2.5 kg); known to reach a length of 36 inches (91 cm). **COLOR:** Bright vermilion above, sometimes blotched with black, fading to

light below; smaller specimens often have a whitish streak along lateral line. All fins except spinous dorsal are usually edged with black; eye bright yellow. □ One of the larger and more colorful of the rockfish species. Found over shallow and deep reef areas in water 150 to 1,200 feet (45.7-365.8 m) deep. Excellent food species.



100. **STARRY ROCKFISH**, spotted rockfish, chinafish, *Sebastes constellatus* (Jordan and Gilbert). **DISTRIBUTION:** Near Cedros Island, Baja California, Mexico, to San Francisco, Calif. **SIZE:** Reported to attain a length of 18 inches (46 cm); average weight is about 1½ pounds (0.7 kg). **COLOR:** Orange red above, shading to yellow on sides and below; profusely covered with small bright-green spots; three to five white blotches on back. □ A brightly colored species common off southern California, where it is usually taken over deep reefs.



101. **ROSY ROCKFISH**, corsair, dude, scacciatale, scratch-tail, *Sebastes rosenblatti* Girard. **DISTRIBUTION:** Turtle Bay, Baja California, Mexico, to Puget Sound, Wash. **SIZE:** A small species, averaging about ½ pound (0.2 kg). Maximum length reported to 12¼ inches (32 cm). **COLOR:** Yellow, blotched with dark red on back and sides, fading to whitish below; white blotches bordered with purple above lateral line; pinkish fins. □ Taken in deep water (90 fathoms or 164.6 m); sometimes in shallower water over reefs or rocky areas. A good food species, although small in size.



102. **GREENSTRIPED ROCKFISH**, strawberry rock cod, reina, serena, *Sebastes elongatus* Ayres. **DISTRIBUTION:** Cedros Island, Baja California, Mexico, north to Green Island, Alaska. **SIZE:** Small; average weight about ¾ pound (0.3 kg); length recorded to 15 inches (38 cm). **COLOR:** Pale red above, white on sides joining near tail; black on tip of chin;

pinkish fins; pink lateral line. □ A deep-water species (200-1,300 feet or 61.0-396.2 m) usually caught from sport boats fishing over rough bottom.

103.



103. GREENSPOTTED ROCKFISH, chucklehead, Santa Maria, *Sebastes chlorostictus* (Jordan and Gilbert). DISTRIBUTION: Cedros Island, Baja California, Mexico, to Copalis Head, Wash. SIZE: Average weight 1½ pounds (0.6 kg); record length reported to be near 20 inches (51 cm). COLOR: Pinkish yellow with irregular green spots; three to five whitish blotches on back bordered with purple red; purple bar across head behind eyes. □ Adults and young both found over deepwater reef areas.

RED ROCKFISHES OF LESS IMPORTANCE TO THE MARINE ANGLER:

104. COW ROCKFISH, cowcod, roosterfish, gallo, chefra, cowfish, *Sebastes levis* (Eigenmann and Eigenmann). DISTRIBUTION: Central Baja California, Mexico, to near Eureka, Calif. SIZE: One of the largest of the rockfishes, reaching 37 inches (94 cm) long and a weight of 28½ pounds (12.9 kg). COLOR: Yellowish red with faint vertical bars on adults.

105. STRIPETAILED ROCKFISH, popeye rockfish, bigeye rockfish, oliveback rockfish, *Sebastes saxicola* (Gilbert). DISTRIBUTION: Viscaino Bay, Baja California, Mexico, to southeastern Alaska. SIZE: Length to 15¼ inches (39 cm). COLOR: Tail has green stripes in membranes.

STRIPED ROCKFISHES:

106. TREEFISH, convictfish, barberpole, *Sebastes serriceps* (Jordan and Gilbert). DISTRIBUTION: Central Baja California, Mexico, to San Francisco, Calif. SIZE: Length reported to 16 inches (41 cm). COLOR: Olive brown above to yellowish below, with five to six vertical black bars on sides reaching to belly. □ This colorful rockfish, although minor in the sport catch, is common off southern California in relatively shallow water out to about 150 feet (45.7 m) deep.

107. FLAG ROCKFISH, Spanish flag, barberpole, hollywood, convictfish, shoflies, tiger, *Sebastes rubrivinctus* (Jordan and Gilbert). DISTRIBUTION: Cape Colnett, Baja California, Mexico, to San Francisco; records north of San Francisco may be the redbanded rockfish, *Sebastes babcocki*. SIZE: Length to 25 inches (64 cm). COLOR: As name indicates, has four vertical red stripes on cream-white background.

30

SCORPIONFISHES:

108.



108. CALIFORNIA SCORPIONFISH, sculpin (not related to the sculpin family, Cottidae), *Scorpaena guttata* Girard. DISTRIBUTION: Near Magdalena Bay, Baja California, Mexico, to Santa Cruz, Calif. SIZE: Length recorded to about 17 inches (43 cm). COLOR: Brick red to brown; numerous dark spots and blotches on body, head, and fins. □ An inshore fish common in bays and along shores throughout the year in southern California; however, spring and summer appear to be best fishing season. Although it sometimes occurs over sandy or sandy-mud bottom, this species seems to prefer rocky surroundings and water shallower than 100 feet (< 30.5 m). Fish should be handled with care; spines (dorsal, anal, and pelvic) are venomous and can inflict very painful wounds. Experienced anglers handle by inserting thumb in fish's mouth and holding by lower jaw. An excellent food fish.

ANOPOLOMATIDAE: SABLEFISHES

109.



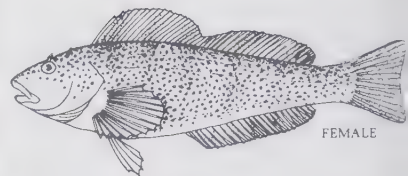
109. SABLEFISH, black cod, mackerel, coal cod, butterfish, blue cod, skil, *Anoplopoma fimbria* (Pallas). DISTRIBUTION: Cedros Island, Baja California, Mexico, to northwestern Alaska, Bering Sea, and Japan. SIZE: Catches of young fish average ¼ to ½ pound (0.1-0.2 kg), while adults may weigh up to 30 pounds (13.6 kg); a record length is reported to 40 inches (102 cm). COLOR: Adults are blackish gray above, shading to lighter gray or white below. Coloration in young is more defined with dark blue or green above, white on belly. □ Young fish are sometimes found nearshore; however, adults live in deep water up to 400 feet (122 m) or more. They appear to migrate into shallower water during summer. An important species in northern California and off Oregon and Washington, although a small restricted fishery does exist off Newport Bay in southern California. This species is frequently caught in the same area as the Pacific halibut, and is an excellent food fish.

HEXAGRAMMIDAE: GREENLINGS

110.



MALE



FEMALE

110. KELP GREENLING, greenling sea-trout, kelpfish, rock trout, *Hexagrammos decagrammus* (Pallas). DISTRIBUTION: La Jolla, Calif., to Aleutian Islands, Alaska. SIZE: Length up to 21 inches (53 cm); however, usual catch is about 12 inches (30 cm) long. COLOR: Males are dark gray with sky-blue spots on head and fore part of body. Females are gray brown with uniform reddish or golden-brown spots on head and body. □ This species is found around rocky shores, reefs, and kelp bed areas. Common along jetties and most abundant off northern California, Oregon, Washington, and Alaska. Excellent food fish.

111.



111. ROCK GREENLING, red greenling, fringed greenling, *Hexagrammos lagocephalus* (Pallas). DISTRIBUTION: Point Conception, Calif., to Alaska and Bering Sea. Abundant off Oregon northward to Alaska. SIZE: Length recorded up to 24 inches (61 cm). Weight of the average catch is about ¼ pound (0.3 kg). COLOR: Highly variable, usually reddish brown with darker mottling, sometimes large red blotches on sides; tail fin tipped with red; dark round spot above pectoral fin; inside of mouth bluish. □ A shallow-water species, inhabiting much the same areas as the kelp greenling (rocky shores, jetties, etc.).

112.



112. LINGCOD, cultus cod, buffalo cod, green cod, ling, bocallao, *Ophiodon elongatus* Girard. DISTRIBUTION: Point San Carlos, Baja California, Mexico, to Kodiak Island, Alaska. SIZE: Average weight is about 8 pounds (3.6 kg); however, they are reported to attain at least 50 inches (127 cm) in length and a weight of

50 pounds (22.7 kg). COLOR: Extremely variable with habitat. Ground color may be gray brown, blue to green, or black. Mottlings, spots, and other markings are not specific. □ Common to central California northward, off Oregon, Washington, and southeastern Alaska coasts. A desirable food species. Young lingcod are caught near rocky or kelp bed areas. Adults tend to frequent deeper water up to 350 feet (106.7 m) in areas of rough bottom.

113.



113. ATKA MACKEREL, *Pleurogrammus monopterygius* (Pallas). DISTRIBUTION: Monterey Bay, Calif., to northwestern Alaska, Bering Sea, and Sea of Japan. SIZE: Attains a length of up to 2 feet (61 cm), although the average length is about 12 inches (30 cm). COLOR: Dusky yellow with five blackish vertical bars crossing sides; ventral and anal fins dark. □ An important game species in Alaska, commonly taken near the surf zone, around rocky and kelp bed areas, and in semisheltered water. Often found in large schools.

GREENLINGS OF LESS IMPORTANCE TO THE MARINE ANGLER:

114. WHITESPOTTED GREENLING, *Hexagrammos stelleri* Tilesius. DISTRIBUTION: Puget Sound, Wash., to Japan. SIZE: Length to at least 19 inches (48 cm). COLOR: Light brown to greenish, often with reddish tinge; conspicuous white spots on body.

115. PAINTED GREENLING, *Oxylebius pictus* Gill. DISTRIBUTION: Point San Carlos, Baja California, Mexico, to Strait of Georgia, British Columbia. SIZE: Length to at least 10 inches (25 cm). COLOR: Brown and dark-red bars and mottling over grayish-brown body; flaps on head are red. Rarely taken.

COTTIDAE: SCULPINS

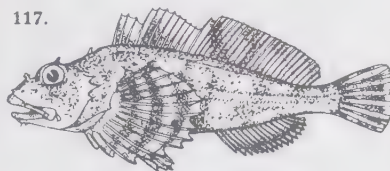
116.



116. CABEZON, bullfish, bullhead, blue cod, bull cod, marbled sculpin, *Scorpaenichthys marmoratus* (Ayres). DISTRIBUTION: Point Abreojos, Baja California, Mexico, to Sitka, Alaska. SIZE: Average weight is about 2 pounds (0.9 kg). Largest fish reported was 39 inches (99 cm) long and weighed slightly over 15 pounds (6.8 kg). COLOR: Highly variable from

brown to red, greenish or gray, usually with extensive mottling or blotching. Mouth lining in females usually green, males red. □ The flesh of the cabezon has an excellent flavor, but the roe is reported to be poisonous. This fish is found over many types of bottom, usually rock and sand, in shallow water out to depths of about 250 feet (76.2 m).

117.



117. RED IRISH LORD, *Hemilepidotus hemilepidotus* (Tilesius). DISTRIBUTION: Monterey Bay, Calif., to Sea of Okhotsk. SIZE: Average weight about ½ pound (0.2 kg); greatest reported length is 20 inches (51 cm), but is not common over 12 inches (30 cm). COLOR: Dusky to bright red above, becoming lighter below; mottled with brownish red and profusely covered with brownish to black spots. □ Fleshy flaps on snout and just above eyes. A rocky-shore species common to Oregon, Washington, and Alaska. Ranges from shallow intertidal areas out to 156 feet (47.5 m). Feeds on crabs, barnacles, and mussels.

118.



118. PACIFIC STAGHORN SCULPIN, bullhead, smooth sculpin, *Leptocottus armatus* Girard. DISTRIBUTION: San Quintin Bay, Baja California, Mexico, to Chignik, Alaska. SIZE: Length to 12 inches (30 cm). COLOR: Greenish brown or gray above, white to yellow below. □ This abundant inshore sculpin, although sometimes considered a nuisance to fishermen, is an important baitfish in California. Common in bays and brackish-water areas.

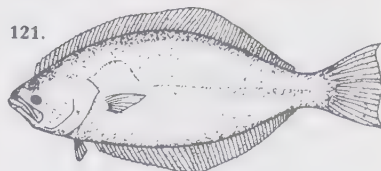
SCULPINS OF LESS IMPORTANCE TO THE MARINE ANGLER:

119. BROWN IRISH LORD, *Hemilepidotus spinosus* (Ayres). DISTRIBUTION: Southern California to Puffin Bay, Alaska. SIZE: Length to 10 inches (25 cm). COLOR: Light to dark brown with dark mottling.

120. BUFFALO SCULPIN, *Enophrys bison* (Girard). DISTRIBUTION: Monterey Bay, Calif., to Kodiak Island, Alaska. SIZE: Length to 12 inches (30 cm). COLOR: Dark gray green or brown above; purplish bony plates on head and on lateral line.

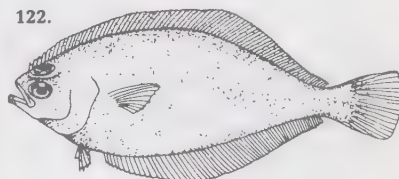
BOTHIDAE: LEFTEYE FLOUNDERS

121.



121. CALIFORNIA HALIBUT, southern halibut, *Paralichthys californicus* (Ayres). DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to British Columbia. SIZE: Record size is about 5 feet (152 cm) and 72 pounds (32.7 kg). Average size 6 to 7 pounds (2.7-3.2 kg); however, pier-caught fish are usually much smaller (called "fly-swatters"). COLOR: Olivaceous black to brown, sometimes with lighter or darker mottling; young often with whitish spots. Blind side is unpigmented. □ Common along sandy shores and nearshore shelves in southern California; some also are taken in the Morro Bay, Monterey Bay, and in the San Francisco area. An important species to pier anglers in southern California. Good fishing is sometimes found near live-bait receiver locations. Rarely taken in water over 10 to 15 fathoms (18.3-27.4 m) deep. In southern California common along shore in the spring, frequenting channels leading into larger bays and just outside the surf zone. From Morro Bay north to San Francisco and Tomales bays, fishing is best in summer and early fall.

122.



122. PACIFIC SANDDAB, mottled sanddab, *Citharichthys sordidus* (Girard). DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to northwestern Alaska and Sea of Japan. SIZE: To 16 inches (41 cm) long; most weigh less than ½ pound (0.2 kg). COLOR: Various shades of light brown, sometimes mottled with dull orange, yellow, or black. Blind side is unpigmented. □ Common over sandy or muddy-sand bottoms at depths of 20 to 50 fathoms (36.6-91.4 m). An excellent food fish.

PLEURONECTIDAE: RIGHTEYED FLOUNDERS

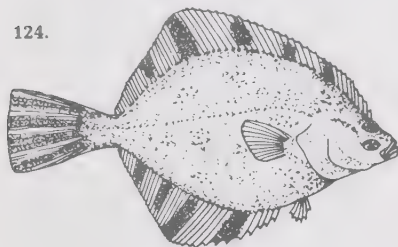
123.



123. PACIFIC HALIBUT, northern halibut, *Hippoglossus stenolepis* Schmidt. DISTRIBUTION: Santa Rosa Island, Calif., to the Bering Sea and Sea of Japan. SIZE:

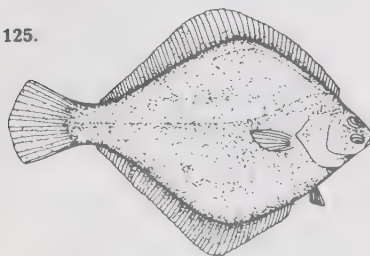
Average weight of the sport catch off the Washington, Oregon, and northern California coasts is 5 pounds (2.3 kg), but larger fish are common in Alaska. Females recorded to 495 pounds (224.5 kg), males to 123 pounds (55.8 kg). Length up to 8½ feet (259 cm). COLOR: Uniform dark brown to black, sometimes with paler blotches and fine mottling. Blind side is unpigmented. □ Commonly caught off Oregon, Washington, and Alaska; not usually taken south of extreme northern California. Fished in moderately deep water, 20 to 100 fathoms (36.6-182.9 m). Sometimes appears in relatively shallow water during summer. An excellent food species.

124.



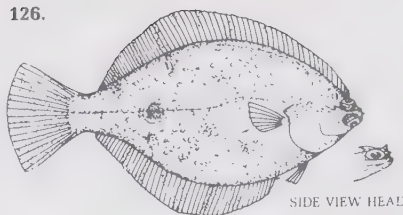
124. STARRY FLOUNDER, diamondback, *Platichthys stellatus* (Pallas). DISTRIBUTION: Santa Barbara, Calif., to Arctic Alaska and Sea of Japan. An abundant species from central California north to Alaska. SIZE: Weight recorded up to 20 pounds (9.1 kg) and a length of 3 feet (91 cm). However, the average sport-caught fish is about 1¼ pounds (0.6 kg). COLOR: Mottled dark brown with alternating white to light orange and black bands on dorsal and anal fins. Blind side is unpigmented. □ One of the few flounder species that may ordinarily have the eyes and color on either side. One of the most important sport-caught flatfishes along the entire Pacific coast. Lives in shallow water over sandy or mud bottom. Sometimes caught at depths of up to 70 fathoms (128.0 m). It is common in bays, and frequently migrates into tidewater areas and up rivers. Has a very rough (grindstone) skin.

125.



125. DIAMOND TURBOT, *Hypsopsetta guttulata* (Girard). DISTRIBUTION: Gulf of California and Magdalena Bay, Baja California, Mexico, to Cape Mendocino, Calif. SIZE: Record length is about 18 inches (46 cm); average weight of the sport catch is about 1¼ pounds (0.6 kg). COLOR: Gray to brown, mottled with blue spots. Blind side is unpigmented. □ Commonly found in bays and sloughs over mud and sand bottom. Usually caught in water less than 500 feet (152.4 m) deep. Best fishing is in southern California in such locations as Newport and Mission bays, where it is caught year-round.

126.



SIDE VIEW HEAD

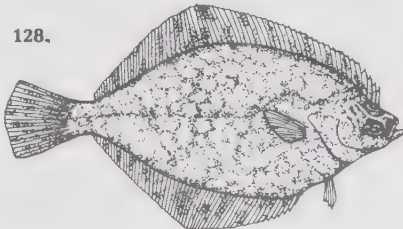
126. HORNYHEAD TURBOT, *Pleuronichthys verticalis* Jordan and Gilbert. DISTRIBUTION: Magdalena Bay, Baja California, Mexico, to Point Reyes, Calif. SIZE: Length recorded to 14½ inches (37 cm), average weight about ¾ to 1 pound (0.3-0.5 kg). COLOR: Brown with darker mottlings and scattered pale blotches. □ Common to southern California in bays, sloughs, and other nearshore areas. Similar in habitat preference to the diamond turbot.

127.



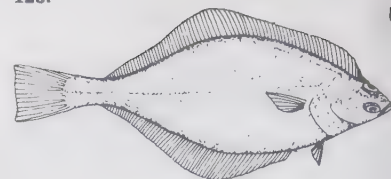
127. PETRALE SOLE, roundnose flounder, *Eopsetta jordani* (Lockington). DISTRIBUTION: Coronado Islands, Baja California, Mexico, to northern Gulf of Alaska. SIZE: Average weight is about 1¼ pounds (0.8 kg); maximum recorded length is 27½ inches (70 cm). COLOR: Uniform dark to light brown, sometimes with paler blotches. Blind side is unpigmented. □ An important and desirable food fish caught off central California, Oregon, and Washington coasts. It is commonly found on sand and mud bottoms, usually in depths of 60 feet (18.3 m) or more during the summer, migrating to deeper water (up to 1,200 feet or 365.8 m) during the winter.

128.



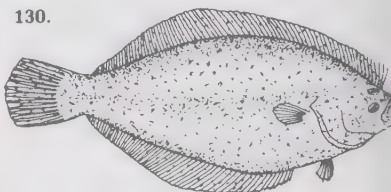
128. ROCK SOLE, broadfin flounder, *Lepidopsetta bilineata* (Ayres). DISTRIBUTION: Southern California to the Bering Sea and Sea of Japan. SIZE: Record length is about 22½ inches (57 cm); average weight is about 1¼ pounds (0.6 kg). COLOR: Dark to light brown with lighter or darker yellow or red mottlings and spots; fins with dark blotches or bars. Blind side is unpigmented. □ Known to range to a depth of about 70 fathoms (128 m), but is frequently caught in shallow water over sandy or gravelly bottom, and sometimes near eel grass beds. Most abundant from central California north into Puget Sound.

129.



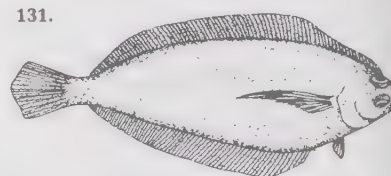
129. ENGLISH SOLE, lemon sole, pointed nose flounder, *Parophrys vetulus* Girard. DISTRIBUTION: Central Baja California, Mexico, to northwestern Alaska. SIZE: Average weight about 1 pound (0.5 kg); record length is reported to be 24 inches (61 cm). COLOR: Brown, with fins edged with darker brown to black. Blind side is unpigmented. □ An important species from central California north. Migratory, found in bays and estuaries out to about 200 fathoms (365.8 m). Caught nearshore during the summer, and, although sometimes taken from piers and off jetties at this season of the year, more are landed by skiff and party boat anglers than by any other method. A good food fish; however, the flesh of inshore specimens sometimes has an iodine flavor.

130.



130. SAND SOLE, fringe flounder, *Psetichthys melanostictus* Girard. DISTRIBUTION: Point Mugu, Calif., to northwestern Gulf of Alaska. SIZE: Average weight ¼ pound (0.2 kg); record length reported to be 21 inches (53 cm). COLOR: Dark gray to brown, speckled with dark brown or black spots. □ This inshore species is usually caught along sandy shores, around jetties, and in estuaries. The young are sometimes caught around rocky areas in summer. Migrates to deep water in the winter. Common north of Point Conception, Calif.

131.



131. REX SOLE, longfin sole, *Glyptocephalus zachirus* Lockington. DISTRIBUTION: San Diego, Calif., to the Bering Sea. SIZE: Average weight is about ½ pound (0.2 kg); maximum length is reported to be about 23¼ inches (59 cm). COLOR: Uniform light brown on eyed side; fins darker, pectoral fins black. Blind side is unpigmented. □ A deepwater species, usually caught over sand and sand-mud bottom. Similar in habitat requirements to the petrale sole and Pacific sanddab. A highly desirable food species.

**FLATFISHES OF LESS IMPORTANCE
TO THE MARINE ANGLER:**

132. **CURLFIN SOLE**, *Pleuronichthys decurrens* Jordan and Gilbert. **DISTRIBUTION:** San Quintin Bay, Baja California, Mexico, to northwestern Alaska. **SIZE:** Length to 14½ inches (37 cm). **COLOR:** Reddish brown with darker brown or gray mottling above.

133. **SPOTTED TURBOT**, *Pleuronichthys ritteri* Starks and Morris. **DISTRIBUTION:** Magdalena Bay, Baja California, Mexico, to Point Conception, Calif. **SIZE:** Length to 11½ inches (29 cm). **COLOR:** Brown to gray with light speckling; usually with three dark spots.

134. **C-O SOLE**, *Pleuronichthys coenosus* Girard. **DISTRIBUTION:** Cape Colnett, Baja California, Mexico, to southeastern Alaska. **SIZE:** Length to about 14 inches (36 cm). **COLOR:** Dark brown above mottled with light brown.

135. **BUTTER SOLE**, *Isopsetta isolepis* (Lockington). **DISTRIBUTION:** Southern California to Alaska and Bering Sea, rare south of Point Conception, Calif. **SIZE:** Length to 21¼ inches (55 cm). **COLOR:** Dark to light brown or gray with light mottling, sometimes with yellow or green spots; fins edged with yellow.

136. **SLENDER SOLE**, *Lyopsetta exilis* (Jordan and Gilbert). **DISTRIBUTION:** Cedros Islands, Baja California, Mexico, to Alek Canyon, Alaska. **SIZE:** Length to 13 inches (33 cm). **COLOR:** Uniform light olive brown.

137. **DOVER SOLE**, *Microstomus pacificus* (Lockington). **DISTRIBUTION:** San Cristobal Bay, Baja California, Mexico, to Bering Sea. **SIZE:** Length to 30 inches (76 cm). **COLOR:** Uniform gray brown; fins black.

OTHER MINOR MARINE GAME FISHES:

A brief listing is given below of some additional families and species of fishes which now do not contribute significantly to the sport catch, but sometimes are taken by Pacific coast anglers. This listing is not complete since marine anglers capture many species during the course of the year that are not listed here, but it reviews some of the more commonly caught minor species.

SCYLIORHINIDAE: CAT SHARKS

138. **SWELL SHARK**, *Cephaloscyllium ventriosum* (Garman). **DISTRIBUTION:** Chile to Monterey, Calif. Not common north of Point Conception, Calif.

SQUALIDAE: DOGFISH SHARKS

139. **SPINY DOGFISH**, *Squalus acanthias* Linnaeus. **DISTRIBUTION:** Temperate and subtropical Atlantic and Pacific oceans; in the eastern Pacific, in Chile, southern California to Alaska, and to Japan.

RAJIDAE: SKATES

140. **BIG SKATE**, *Raja binoculata* Girard. **DISTRIBUTION:** San Quintin Bay, Baja California, Mexico, to northwestern Alaska and Bering Sea. Not common south of Point Conception; Calif.

141. **CALIFORNIA SKATE**, *Raja inornata* Jordan and Gilbert. **DISTRIBUTION:** Turtle Bay, Baja California, Mexico, to the Strait of Juan de Fuca.

142. **LONGNOSE SKATE**, *Raja rhina* Jordan and Gilbert. **DISTRIBUTION:** Point Loma, Calif., to Southern Alaska.

DASYATIDAE: STINGRAYS

143. **ROUND STINGRAY**, *Urolophus halleri* Cooper. **DISTRIBUTION:** Panama Bay, Panama, to Humboldt Bay, Calif. Rare north of Point Conception, Calif.

MURAENIDAE: MORAYS

144. **CALIFORNIA MORAY**, *Gymnothorax mordax* (Ayres). **DISTRIBUTION:** Magdalena Bay, Baja California, Mexico, to Point Conception, Calif.

CLUPEIDAE: HERRINGS

145. **PACIFIC HERRING**, *Clupea harengus pallasi* Valenciennes. **DISTRIBUTION:** Northern Baja California, Mexico, to northern Eurasia, Bering Sea, and Japan.

146. **PACIFIC SARDINE**, *Sardinops sagax caeruleus* (Jenyns). **DISTRIBUTION:** Guaymas, Gulf of California, Mexico, to Kamchatka Peninsula, USSR.

ENGRAULIDAE: ANCHOVIES

147. **NORTHERN ANCHOVY**, *Engraulis mordax* Girard. **DISTRIBUTION:** La Paz, Baja California, Mexico, to Queen Charlotte Island, British Columbia.

SYNODONTIDAE: LIZARDFISHES

148. **CALIFORNIA LIZARDFISH**, *Synodus lucioceps* (Ayres). **DISTRIBUTION:** Guaymas, Gulf of California, Mexico, to San Francisco, Calif. Uncommon north of Point Conception, Calif.

BATRACHOIDIDAE: TOADFISHES

149. **PLAINFIN MIDSHIPMAN**, northern midshipman, *Porichthys notatus* Girard. **DISTRIBUTION:** Gorda Bank, Gulf of California, Mexico, to Sitka, Alaska.

POMADASYIDAE: GRUNTS

150. **SALEMA**, bigeye bass, *Xenistius californiensis* (Steindachner). **DISTRIBUTION:** Peru north to Monterey Bay, Calif. Rare north of Point Conception, Calif.

POMACENTRIDAE: DAMSELFISHES

151. **BLACKSMITH**, *Chromis punctipinnis* (Cooper). **DISTRIBUTION:** Point San Pablo, Baja California, Mexico, to Monterey, Calif.

CLINIDAE: CLINIDS

152. **GIANT KELPFISH**, *Heterostichus rostratus* Girard. **DISTRIBUTION:** Cape San Lucas, Baja California, Mexico, to British Columbia.

153. **ONESPOT FRINGEHEAD**, *Neoclinus uninotatus* Hubbs. **DISTRIBUTION:** San Diego Bay to Bodega Bay, Calif.

Marine Game Fishes of the Pacific Islands

The following pages describe some of the major game fishes taken in marine and brackish waters of Hawaii, American Samoa, and Guam. It is indeed unfortunate that these tropical fishes could not be reproduced in color, for they are among the most beautiful in the world.

The local fish names are given first, since it is by these names that they are known in the tropical Pacific. Usually the Hawaiian name is given first, identified by the symbol (H), followed by its equivalent in Samoan (S) or Guamanian (G), and then by its English equivalent if one exists. The authorized scientific name and the name of the person who originally

described the species are given last.

For those who wish to pronounce the Hawaiian names correctly, it is relatively simple. There are only 12 letters in the alphabet and the five vowels, A, E, I, O, U, are pronounced: a as in father, e as in vein, i as in peep, o as in own, and u as in book. Each vowel is pronounced. For instance, aholehole is pronounced ah-ho-leh-ho-leh, with the accent on the second and fourth syllable. The consonants are pronounced as in English, except that W, especially when after the first syllable, has the sound of V as in valuable. For example 'aweoweo is pronounced ah-veh-oh-veh-oh. The apostrophe or hamza, as

in 'aweoweo and in other Hawaiian fish names, indicates elision of one or more letters. It does not indicate accent, but a break in sound between the letters it separates. In writing Hawaiian names it is important that these marks be used, since they are an essential part of the word.

Marine anglers wishing to make a closer species identification of their catch should read Handbook of Hawaiian Fishes by Gosline and Brock (1960, University Press, Honolulu). This reference is the best available covering most of the species. Other references for specific families and genera will be found in the section on Reference.

CARCHARINIDAE: REQUIEM SHARKS

154.



154. MANO (H), malie (S), tanifa (S), gray shark, sand shark, whaler, *Carcharhinus* spp. DISTRIBUTION: Members of this genus are widely distributed in tropical and temperate seas worldwide. SIZE: The species above, the gray reef shark, *C. amblyrhynchos* (Bleeker), reaches a length of about 8 feet (244 cm); other Pacific members of this genus are reported to reach up to 16 feet (488 cm). COLOR: Differs with species; generally grayish to brownish, fading to lighter below. □ Most "typical" sharks belong to this group; many are inshore or reef-inhabiting species; others also occur far out at sea. A few are considered potentially dangerous to humans and attain considerable size. Although sometimes considered a nuisance to anglers, sharks are rapidly growing in popularity as game fishes. The gray reef shark is especially abundant around American Samoa. It also occurs around Hawaii and Guam, but is not sought by anglers. Sharks are usually caught by handlining at anchor or adrift and by trolling over channel areas between reefs and over offshore ledges.

SPHYRNIIDAE: HAMMERHEAD SHARKS

155.



155. MANO KIHIKIHI (H), kiluus (G), mata-i-taliga (S), scalloped hammerhead (shark), *Sphyrna lewini* (Griffith and Smith). DISTRIBUTION: Tropical and temperate Atlantic, Pacific, and Indian oceans. SIZE: Reaches a length of over 10 feet (305 cm). COLOR: Light gray above and white below; black on the ventral surfaces of the pectoral fins. □ This shark occurs inshore as well as offshore, and although sometimes found in large aggregations, it is usually solitary. Taken by anglers in Hawaii and American Samoa; only rarely taken in Guam. Caught by trolling or drifting with whole or cut baits. Rarely eaten, sometimes used as bait.

ELOPIDAE: TARPONS, LADYFISHES

156.



156. AWAAWA (H), awa'aua (H), pake 'awa (H), ladyfish, tenpounder, *Elops hawaiiensis* Regan. DISTRIBUTION: Tropical Pacific. SIZE: Up to about 24 inches (61 cm), usually about 12 to 15 inches (30-38 cm). COLOR: Bright silvery, with a blue-green hue on the dorsal area. □ The awaawa is primarily an inshore fish, often found in bays and harbors and along sandy shores. In Hawaii it is

known to enter streams and rivers and is commonly reared in fish ponds. This species rarely occurs in American Samoa and Guam. Taken by hook and line and by gill net throughout the Hawaiian Islands. Excellent light-tackle quarry that fights gamely and leaps repeatedly when hooked. The awaawa is edible, but the flesh contains many fine bones. Widely used by the Chinese in making fish cakes.

ALBULIDAE: BONEFISHES

157.



157. 'O'IO (H), bonefish, *Albula vulpes* (Linnaeus). DISTRIBUTION: Worldwide in tropical and subtropical oceans. SIZE: All-tackle record (Zululand, South Africa) is 19 pounds (8.6 kg) and 39 5/8 inches (100.7 cm) long. In the Pacific Ocean (Kauai, Hawaii) the record is 18 pounds 2 ounces (8.2 kg), and a length of 3 feet 5 1/2 inches (105.4 cm). Hawaiian bonefish are usually about 15 to 18 inches (38-46 cm) long. COLOR: Bright iridescent silver. □ The 'o'io is a schooling fish that feeds along sandy bottom, usually over sand patches or channels between coral formations in the reef. Sometimes enters the surge zone along beaches. Although caught throughout the year in Hawaii, the season usually begins in December when the fish come fairly close to shore to spawn, and fishing is usually good through April. Exceptionally large fish have been taken from waters off Kauai, Oahu, and Maui. This species is uncommon in American Samoa and does not occur in Guam. Caught surf casting and bottomfishing with cut bait; some are taken with gill nets. Like the awaawa, the flesh of the bonefish is

palatable, but contains numerous fine bones. It is, however, a Hawaiian favorite for making fish cakes and poki (raw, spiced).

CHANIDAE: MILKFISHES

158.



158. AWA (H), agaa (G), milkfish, *Chanos chanos* (Forskål). DISTRIBUTION: Throughout the tropical Indo-Pacific. SIZE: Up to 3 feet (91 cm) long; most caught are around 18 to 24 inches (46-61 cm). COLOR: Silvery. □ The awa is a schooling surface-feeding fish, common to brackish-water areas, bays, and inlets in the Hawaiian Islands. Common in American Samoa, but very rarely fished for; uncommon in Guam. Hawaiian anglers catch awa with hook and line using bread or algae for bait. Like the awaawa and the 'o'io, this fish is a scrappy fighter, often leaping from the water when hooked. Also taken with gill nets; young fish are sometimes taken with cast nets. Considered a fine food fish; some are raised commercially in fish ponds in Hawaii.

MURAENIDAE: MORAY EELS

159.



159. PUHI (H), puihi-paka (H), pusi (S), titugi (G), moray, *Gymnothorax* spp. DISTRIBUTION: Tropical Pacific Ocean. SIZE: Hawaiian morays range up to 5 or 6 feet (152-183 cm) long but most are under 2 feet (61 cm). □ This group contains all puihi or morays most commonly seen in Hawaiian waters and in the market. The fish illustrated above, *G. flavimarginatus* (Rüppell), the puihi-paka, is one of Hawaii's larger eels and relatively common. Morays are pugnacious predators and have large fanglike teeth. Some are known to bite viciously—but usually only when provoked. Most of the time they remain deep in crevices and holes in reefs and rocky areas where they lie in wait for passing or injured prey. Most are speared, some are taken incidentally by hook and line and in traps. Commonly caught for food in American Samoa, but not sought after in Guam where the flesh is reported to be occasionally poisonous. Sometimes used as bait in Hawaii.

BELONIDAE: NEEDLEFISHES

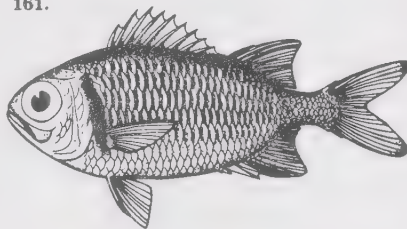
160.



160. 'AHA'AHA (H), ise (S), keeltail needlefish, needlefish, *Platybelone argalus* (Lesueur). DISTRIBUTION: Worldwide. SIZE: Attains a length of about 15 inches (38 cm). COLOR: Blue green on back, fading to silvery below. □ A near- and offshore schooling species, often seen skittering or gliding over the water's surface. Common in Hawaii and American Samoa, although not sought after by Samoan fishermen. In Guam, a much larger species of needlefish called "pulus" or houndfish, *Tylosurus crocodilus* (Peron and Lesueur), is one of the more common fishes taken with spinning gear. In general, needlefish are taken by pole and line using artificial lures or live bait. The greenish flesh of the 'aha'aha is reported to have a very good flavor.

HOLOCENTRIDAE: SQUIRRELFISHES

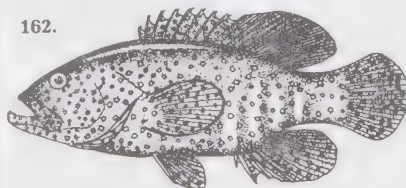
161.



161. MENPACHI (H), 'u'u (H), malau (S), sasag (G), squirrelfish, *Myripristis berndti* Jordan and Evermann and *M. amaenus* (Castelnau). DISTRIBUTION: Tropical Pacific Ocean. SIZE: Up to 14 inches (36 cm); averages 7 to 9 inches (18-23 cm). COLOR: Bright red. □ These two species of menpachi are common inshore reef fishes in Hawaii. Both are nocturnal and congregate in caves and deep crevices during the day, venturing out over the reef at night to feed. Usually taken with spears; also with gill nets and hooks and lines and in traps. Fished for mostly at night. Menpachi are highly esteemed as food fish and subsequently bring a high price at Hawaiian markets.

SERRANIDAE: SEA BASSES

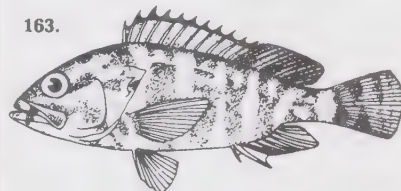
162.



162. ROI (H), gatala moana (S), gadao (G), blue spotted grouper, *Cephalopholis argus* Bloch and Schneider. DISTRIBUTION: Tropical Indo-Pacific. SIZE: Reaches about

20 inches (51 cm) long. COLOR: Purple brown with light-blue spots. Pale bars evident towards tail region as indicated. □ A very common bottomfish in American Samoa, found over reefs and rocky areas at about 10 to 40 fathoms (18.3-73.2 m). Roi also occurs in Guam and in 1956 was introduced to the Hawaiian Islands where it has now become established around most of the larger islands. Caught handlining on the bottom or spearing. Like most groupers, when hooked this fish usually attempts to get into holes or crevices, so it is wise to keep the fish's head up and the line taut.

163.



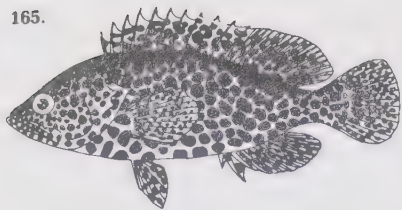
163. GADAO (G), gatala (S), *Epinephelus fasciatus* (Forskål). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Reported to reach about 14 inches (36 cm). COLOR: Red with dusky crossbars which tend to fade with age. Distinguished by the black margin on the spiny dorsal fin. □ A common grouper caught by spinning gear and spears around Guam and American Samoa. Introduced to Hawaii in 1958 from the Marquesas Islands, but did not become established. A good food fish.

164.



164. 'ATA'ATA (S), *Epinephelus tauvina* (Forskål). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 500 pounds (226.8 kg) in weight and averages anywhere from 100 to 400 pounds (45.4-181.4 kg). COLOR: Young fish are tan with irregular brown bars and red mottling and spotting; large specimens are uniform dark brown. □ This large Samoan grouper is common over rocky areas in water from 50 to 500 feet (15.2 to 152.4 m) deep, and is taken by handline. A large unidentified grouper caught by Guam handliners might be closely related to the Samoan species, although its positive identification has yet to be determined. This Guam grouper is reported to reach over 80 pounds (36.3 kg) and is excellent eating. When fresh, it has several broad faint vertical bars on the body which fade soon after death to a uniform dark brown.

165.



165. GATALA (S), gadao (G), grouper, *Epinephelus merra* Bloch. DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 18 inches (46 cm). COLOR: Yellowish white with dark orange-brown spots; more yellow in the dorsal region. □ A very abundant inshore reef-inhabiting grouper in American Samoa and Guam, and one of the two most common groupers taken spearing and with spinning gear over Guam's shallow reefs. Once introduced to Hawaii from Tahiti, but did not become successfully established. Food value considered good.

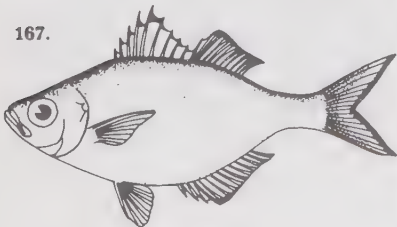
166.



166. GATALA (S), i'a manaia (S), gadao (G), grouper, *Variola louti* (Forsskål). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Reported to reach 3 feet (91 cm) long. COLOR: Yellowish brown or orange, everywhere spotted with small reddish or pinkish spots with those toward the back margined with a purple or blue line. Pectoral and tail fins bright yellow; eye red; underside of head and body red. □ This brilliantly colored grouper occurs both in American Samoa and Guam, and is very common around American Samoa over reef and ledge areas at about 10 to 40 fathoms (18.3-73.2 m). Young fish frequent shallow-water reefs and sometimes enter deep tide pools in American Samoa; in Guam the young of this species appear to prefer deeper water. In Samoa they are caught handlining and sometimes trolling; in Guam most are taken by spear fishermen. Considered a fine food fish.

KUHLIIDAE: AHOLEHOLES

167.



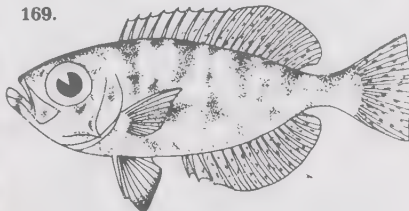
167. AHOLEHOLE (H), mountain bass, silver perch, *Kuhlia sandvicensis* (Steindachner). DISTRIBUTION: Hawaiian Islands. SIZE: Up to 12 inches (30 cm); usually from 4 to 6 inches (10-15 cm). COLOR: Silvery; fins often dusky tipped. □ An abundant inshore fish found in streams, along the shoreline, around pilings

in harbors and bays, or in large schools over reefs. The young are numerous in tide pools while adults inhabit deeper water, but generally no deeper than 20 feet (6.1 m). Aholehole is usually nocturnal and hides in crevices during the day and emerges at night to feed. Taken with cast nets, by hook and line, and by spearing in crevices and holes in the reef. Lights are sometimes used to attract them at night. An excellent food fish.

168. UMATAN (G), sasele (S), *Kuhlia rupestris* (Cuvier and Valenciennes). DISTRIBUTION: Widespread in tropical central Indo-Pacific. SIZE: In Guam this fish may reach 14 to 16 inches (36-41 cm) and up to 1½ to 2 pounds (0.7-0.9 kg); usually runs about 8 to 9 inches (20-23 cm) and about ¼ or ½ pound (<0.3 kg). □ This close relative of the aholehole occurs in American Samoa and is very common to most streams and rivers of Guam. Similar in habits and appearance to *K. sandvicensis*, but seems to have a greater affinity to fresh water. Young umatan are found close to mouths of tributaries while large adults are usually found farther upstream in fresh water. Taken with nets and spears and with light spinning tackle using live bait, artificial flies, and small poppers. An excellent food fish.

PRIACANTHIDAE: BIGEYES

169.



169. 'AWEOWEO (H), mamagas (G), matalupa (S), red bigeye, *Priacanthus cruentatus* (Lacépède). DISTRIBUTION: Circumtropical. SIZE: Up to about 12 inches (30 cm); averages about 6 to 8 inches (15-20 cm). COLOR: Variable; known to change its coloration rapidly from deep red to silvery, or to a mottled silvery pink and red; fins are often speckled with black. □ In Hawaii and American Samoa this nocturnal reef fish is found in shallow reefs and in bays and harbors where it feeds primarily on free-swimming invertebrates and small fishes. It is uncommon in Guam. In Hawaii the 'aweoweo is usually taken during the evening and moonlit nights are considered best. Occasionally great schools of juvenile fish appear nearshore at night, and it was once thought by early Hawaiian islanders that the appearance of these immense schools signified the imminent death of royalty. Taken pole fishing, handlining, and spearing. Opinions about the food value of this fish vary from fair to excellent.

170. 'ALALAU (H), *Priacanthus alalau* Jordan and Evermann. □ This is another member of the bigeye family taken by Hawaiian fishermen. It does not occur as close to shore as the 'aweoweo, usually found in water deeper than 50 feet (over 15.2 m). SIZE: Reaches up to 14 inches (36 cm) long.

APOGONIDAE: CARDINALFISHES

171.



171. 'UPAPALU (H), lansi (G), fo (S), moonlight fish, moonlight Annie, *Apogon menesemus* Jenkins and A. *kallopterus* Bleeker. DISTRIBUTION: Tropical Pacific Ocean. SIZE: Up to 9 inches (23 cm). COLOR: Both purplish with black markings. □ The fish pictured is *A. menesemus*. These two small inshore reef fishes are very common in the Pacific Islands. 'Upapalu are nocturnal and feed on small crustaceans. Males carry eggs in their mouths for incubation. In Hawaii these two cardinalfishes are often taken pole fishing on moonlit nights over the reefs. Food value is considered good.

CARANGIDAE: JACKS AND POMPANOS

172.



172. KAHALA (H), greater amberjack, *Seriola dumerili* (Risso). Two other amberjacks, *Seriola rivoliana* and *S. quinqueradiata*, also occur in Hawaiian waters and may enter the sport catch. DISTRIBUTION: Circumtropical. SIZE: All tackle record (Bermuda) is 149 pounds (67.4 kg) with a length of 71 inches (180.4 cm). Most caught in Hawaii are around 2 feet (61 cm) long and about 8 to 10 pounds (3.6-4.5 kg). COLOR: Light metallic brown with a purplish tinge. When alive, a faint lemon-yellow band extends from the head to the base of tail. □ The kahala inhabits Hawaii's deeper coastal waters between 40 to 100 fathoms (73.2-182.9 m), living near the bottom. The most productive fishing areas seem to be over deep-sea ledges or drop offs. This fish also occurs in Samoa and similar species, if not the same, occur in Guam. Usually caught handlining off shore, although on rare occasions this fish may come close to shore within casting reach of shore anglers. Small fish are considered good eating, large fish only fair.



173. 'OPELU (H), 'opelu-mama (H), machuman (G), mackerel scad, *Decapterus pinnulatus* (Eydoux and Souleyet). This fish is very similar to the Atlantic mackerel scad, *Decapterus macarellus* (Cuvier). DISTRIBUTION: Tropical Pacific Ocean. SIZE: Up to 20 inches (51 cm) in length; usually less than 10 inches (25 cm). COLOR: Bluish or greenish yellow above, silvery below. □ Found in schools near the surface and in mid-water and common to the coastal waters of Hawaii and Samoa; rarely taken in Guam. In Hawaii, the young under 5 inches (<13 cm) long school far out at sea where they often become the prey of aku or skipjack tuna. Caught by hook and line at night and with a special 'opelu lift net during the day. An excellent food fish; also used as bait and live chum for large tuna and marlin.



174. AKULE (H), aji (H), atule (S), atulai (G), hitting (G), mackerel bigeye scad, *Selar crumenophthalmus* (Bloch). In Hawaii, fish up to 5 inches (13 cm) are called "hahalalu" or "halalu"; those about 5 to 7 inches (13-18 cm) called "ma'au"; and those over 7 inches called akule. DISTRIBUTION: Tropical Pacific. SIZE: Up to 15 inches (38 cm); average caught by anglers is under 8 inches (20 cm). COLOR: Olive green on dorsal area, golden or silvery on sides and head; tail fin yellow and a faint spot on gill cover. □ The akule is a schooling fish inhabiting the mid- or surface waters along the coasts of all the islands, the young often coming close to shore into protected bays and harbors. In Hawaii, young fish or "halalu" offer great sport to shore anglers fishing with light spinning tackle and most are caught from about July to December. Adult fish are found offshore where they are netted or handlined in season by commercial fishermen. In American Samoa, this fish occurs throughout most of the year and is caught in lagoons and bays around Tutuila, usually pole fishing from shore and piers and handlining from boats. In Guam, large schools of juveniles occasionally enter bays and are taken with surround nets and sometimes with spinning gear, usually from April to August; larger fish are taken handlining offshore at night during dark moon phases. An excellent food fish.



ADULT



JUVENILE

175. WHITE ULUA (H), ulua kihikihi, kagami ulua (H), thread crevally, *Alectis ciliaris* (Bloch). Previously known as *Carangoides ajax*. A similar species, *Alectis indica* (Rüppell), also occurs in Hawaii and may enter the sport catch. DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 3½ feet (107 cm) long; usually about 10 to 15 pounds (4.5-6.8 kg). COLOR: Adult fish are dusky white, often darker along the dorsal area; young are silvery. □ The juvenile form, called ulua kihikihi, is one of the most beautiful fish in Hawaiian waters, with the first four or five spiny rays of the dorsal and anal fins produced into long trailing streamers. As the fish matures, these spines grow shorter, and in some adults they disappear completely. The young are often found in harbors and other sheltered waters, but upon reaching maturity this once delicate creature assumes a more jacklike appearance, moves to deeper and more open water. Taken from rocky shores with heavy bait-casting gear. Offshore they are frequently caught deepwater trolling or handlining at depths of about 10 to 30 fathoms (18.3-54.9 m). An excellent food fish, served raw or cooked.



176.

176. 'OMAKU (H), Atule mate (Cuvier and Valenciennes). DISTRIBUTION: Tropical Pacific. SIZE: Up to 12 inches (30 cm); averages about 8 to 10 inches (20-25 cm). COLOR: Greenish yellow often with a brassy tinge over silvery sides. □ This jack is found in protected bays and estuaries in Hawaii, and juveniles are very abundant in fall around floating objects. Most 'omaku are caught with light spinning tackle from shore and piers, and handlining from boats from March to October. Fresh and salted anchovy (nehu) is used for bait. Occasionally taken with throw nets and gill nets. Considered an excellent food fish.



177. PA'U'U (H), tarakito (G) (young called "papio" (H), "lupo" (S), or "tarakitiyos" (G), as are the young of other jacks), crevalle, jack crevally, *Caranx ignobilis* (Forskål). DISTRIBUTION: Tropical Indo-Pacific and Red Sea. SIZE: Up to about 3 feet (91 cm). COLOR: Pale olive above with a greenish tinge around the head; sides white; yellow anal fin. □ One of the more common jacks found around the Pacific Islands. The young are caught by shore anglers with pole and line in brackish-water bays and harbors throughout the islands. In Hawaii live shrimp, or "opae," is used almost exclusively as bait for small fish under 2 pounds (0.9 kg). Adult fish are found over nearshore reefs and are caught casting from rocky shores and ledges and sometimes by spearing. An excellent food fish.



178.

178. 'OMILU (H), hoshi ulua (H), oshi (H), illioli (H), omilumilu (H), malauli (S), tarakito (G), star jack, spotted jack, blue ulua, blue crevally, *Caranx melampygus* Cuvier and Valenciennes. DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 3 feet (91 cm); most fish taken are about 1 to 2 pounds (0.5-0.9 kg). COLOR: Rather variable, usually brownish blue above and silver tan on sides and belly. Fish between 10 and 24 inches (25-61 cm) have many small blackish spots on body; larger fish tend to lose spotting and become more of a uniform dark metallic blue. □ The 'omilu is another very common jack found throughout the Pacific Islands. This fish often moves in close to shore following channels in coral reefs and is taken by shore anglers with surf-casting gear. It is probably the most common ulua caught from shore in Hawaii, especially on the island of Hawaii where it is known locally as illioli. Generally, young fish are found in shallow bays and estuaries while medium-sized fish from 6 to 20 inches (15-51 cm) are taken over reefs. The largest fish are taken with trolling gear just outside the reefs. Also taken spearing, gill netting, and handlining. An excellent food fish.

179.



179. **PAKE ULUA** (H), *mempachi ulua* (H), young called *papio* (H), *tarakito* (G), or *lupo* (S), *Caranx sexfasciatus* Quoy and Gaimard. **DISTRIBUTION:** Tropical Indo-Pacific. **SIZE:** Up to 5 feet (152 cm) or more long; most caught weigh about 2 pounds (0.9 kg). **COLOR:** Dark blue green to gold above; yellow green to silver below. The upper lobe of the caudal fin is black. Juveniles have four to seven dark vertical bars. □ Young fish are found in tide pools and brackish-water areas out to deeper coastal waters; adult fish live along rocky shores in turbulent water and over reefs. In Hawaii, the pake ulua is one of the largest of the jacks taken by anglers but this fish appears to be less common now than in previous years. Caught by hook and line from shore and from boats; adult fish are often taken along with 'opelu and akule while handlining at night. Some are taken by spears. An excellent food fish.

180. **BLACK ULUA** (H), *tarakito* (G), jack, *Caranx lugubris* Poey. **DISTRIBUTION:** Circumtropical. **SIZE:** Up to 3 or 4 feet (91-122 cm) long; average weight about 4½ pounds (2.0 kg). This fish frequents outer reef channels and is similar in appearance to *C. sexfasciatus*, but has a darker body color and an almost black head. □ Caught by anglers in Hawaii and particularly abundant around Guam where they are taken with handlines over bottomfishing areas around the island. Although there are reports of the flesh of this species being poisonous in certain parts of the Atlantic, it is commonly eaten in the tropical Pacific.

181.



181. **KAMANU** (H), Hawaiian salmon, rainbow runner, *Elegatis bipinnulatus* (Quoy and Gaimard). **DISTRIBUTION:** Circumtropical. **SIZE:** The all-tackle record—a fish taken off Kauai—measured 3 feet 11 inches (119.4 cm) and weighed 30 pounds 15 ounces (14.0 kg). Most kamanu caught in the Pacific Islands weigh around 12 to 15 pounds (5.4-6.8 kg). This fish is reported to reach 70 pounds (31.8 kg), although this seems doubtful. **COLOR:** Dark blue above followed in succession down the sides by a light-blue stripe, then a yellow stripe, then another light-blue stripe. Yellowish silver below, fins yellow. □ This sleek and colorful member of the jack family is an open-ocean species, usually seen and caught near the water's surface. Exceptionally large fish are taken in Hawaii, especially off Kauai and Oahu. Also caught off American Samoa and Guam. Caught by trolling with small lures or baits, also with handlines. Excellent eating, cooked or raw.

182.

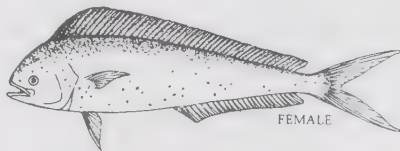


182. **LAE** (H), *lai* (S), *hagi* (G), leather-jacket, runner, leatherback, *Scomberoides lysan* (Forskål). **DISTRIBUTION:** Tropical Indo-Pacific and Red Sea. **SIZE:** Up to 25 inches (64 cm); usually 12 to 15 inches (30-38 cm). **COLOR:** Dusky above, fading to silver on sides and belly. □ The swift-swimming lae is an inshore coastal fish that frequents sheltered bays and harbors and brackish-water areas near the mouths of streams. It feeds at the surface or in mid-water, mostly on smaller schooling fishes. Seldom found very far from shore. In Hawaii, caught with hook and line during the day, often by shore anglers casting bait or lures for young jacks. This fish should be handled carefully because of its sharp venomous anal spines. A good fighter on light tackle. Not widely sought after for food. In Hawaii the tough, leathery skin of the lae is valued for making trolling lures.

CORYPHAENIDAE: DOLPHINS



183.



183. **MAHIMAHI** (H, G), *masimasi* (S), dolphin, *Coryphaena hippurus* Linnaeus. **DISTRIBUTION:** Circumtropical. **SIZE:** All-tackle record (Spanish Wells, Bahamas) is 85 pounds (38.6 kg) with a length of 69 inches (175.3 cm). Hawaiian fish range up to 72½ pounds (32.9 kg), average about 25 pounds (11.3 kg). **COLOR:** When alive the body is brilliant yellow and green dotted with phosphorescent blue, the dorsal fin is purplish blue. This beautiful fish flashes a rainbow of colors when caught, and also just before dying. □ Perhaps this is the best known and most colorful of game fishes and one of the most abundant species caught deep-sea trolling in the Pacific Islands. Mahimahi inhabit the open sea, sometimes swimming in large schools. Commonly seen swimming close to the surface near schools of flying fish on which they feed, or around floating objects. Small fish up to 5 pounds (2.3 kg) are plentiful around the Hawaiian Islands in summer; large fish 30 to 40 pounds (13.6-18.1 kg) are taken February to April. Common off American Samoa and Guam year-round, with best fishing off the western coast of Guam usually from January to April (larger fish are caught later in the season). Males have an almost vertical head profile and grow to larger sizes than the females. Taken trolling and handlining and is as delicious to eat as it is beautiful.

184. **LITTLE MAHIMAHI** (H), pompano dolphin, *Coryphaena equisetis* Linnaeus. **DISTRIBUTION:** Circumtropical. □ This fish is similar in appearance and habits to the mahimahi, but is known to reach a length of only about 30 inches (76 cm). Occasionally taken by Hawaiian anglers.

LUTJANIDAE: SNAPPERS

185.



185. **UKU** (H), *aso'ama* (S), gray snapper, *Aprion virescens* Cuvier and Valenciennes. **DISTRIBUTION:** Tropical Pacific. **SIZE:** Up to 2 feet (61 cm) long; usually about 8 pounds (3.6 kg). **COLOR:** Uniform grayish blue, with the dorsal area more bluish than below. Dark blue towards head; three dark spots near base of dorsal fin. □ Of the large deepwater snappers discussed here, the uku occurs the nearest to shore and in relatively shallow water, usually less than 60 fathoms (109.7 m) deep. It is the most cylindrical of the snappers, having a long head and snout with a rather prominent groove on either side. Taken by hook and line over deep-sea ledges or banks, usually on or near rocky or hard bottom. Some are taken by trolling. An excellent food fish.

186.



186. **'OPAKAPAKA** (H), pink paka (G), pink snapper, *Pristipomoides filamentosus* (Bleeker). **DISTRIBUTION:** Tropical Indo-Pacific. **SIZE:** Up to 3 feet (91 cm) long; and about 18 pounds (8.2 kg); usually 5 to 6 pounds (2.3-2.7 kg). **COLOR:** Light violet brown dorsally, fading to dusky white below; pectoral fin yellowish. Last rays of dorsal and anal fins produced into filaments that reach base of tail fin. □ Like the uku, the 'opakapaka is a deepwater fish, most abundant over rocky bottom drop offs. One of the more common snappers caught over Guam's banks, with most taken at depths of 100 to 150 fathoms (182.9-274.3 m). This fish is also reported to be abundant over the offshore ledges of American Samoa at about 200 to 300 fathoms (365.8-548.6 m), but these bottomfishing areas are seldom fished. In Hawaii, it is generally found in shallower water at around 40 to 100 fathoms (73.2-182.9 m) and young fish are sometimes taken in 20 fathoms (36.6 m). Taken handlining; in Hawaii, most are caught during the winter months. An excellent food fish.

187.



187. YELLOWTAIL KALIKALI (G). *Pristipomoides auricilla* (Jordan, Evermann, and Tanaka). DISTRIBUTION: Tropical Pacific. SIZE: Up to about 18 inches (46 cm) long. COLOR: Body purplish with 17 to 18 narrow, irregular chevron-shaped yellow bands; iris yellow; edge of upper lip yellow; fins yellowish, upper lobe of tail fin with a purple margin. Large males over about 10½ inches (27 cm) have a rather distinct yellow blotch on upper lobe of tail fin. □ A very common deepwater snapper in Guam, caught handlining over offshore ledges and banks at similar depths as *P. filamentosus*. An excellent food fish.

188.



188. YELLOWEYE OPAKAPAKA (G). *Pristipomoides flavipinnus* Shinohara. DISTRIBUTION: Ryukyu and Guam. SIZE: Up to at least 17 inches (43 cm) or more long; fish over 16 inches (41 cm) occur frequently in catch. COLOR: Body lavender brown becoming pale towards belly; eye yellow; snout and head mottled with narrow, irregular, light-yellow streaks. Scales have yellow spots which form thin horizontal stripes above lateral line; fins yellowish. □ This is another common Guam snapper taken at about the same depths as *P. filamentosus* and *P. auricilla*. An excellent food fish.

189.



189. KALIKALI (H), pink kalikali (G). *Pristipomoides sieboldii* (Bleeker). DISTRIBUTION: Tropical Pacific and Indian oceans. SIZE: Up to at least 18 inches (46 cm). COLOR: Light lavender above becoming paler below. Scales above the lateral line have pale-blue spots in the center, forming lengthwise lines that become indistinct toward the belly. Margin of dorsal fin orange with light lavender; tail fin dark lavender with a light margin. □ This offshore snapper is commonly taken around Guam handlining over offshore banks and ledges at depths from 100 to 150 fathoms (182.9-274.3 m); none have been reported from depths less than 100 fathoms (182.9 m). In Hawaii, the kalikali is relatively minor in the sport catch, where it is taken from depths of 60 to 200 fathoms (109.7-365.8 m) with most caught in water 80 to 120 fathoms (146.3-219.5 m). Considered an excellent food fish.

190.



190. ONAGA (H. G), 'ula'ula koae (H. palu (S), red snapper, *Etelis carbunculus* Cuvier. DISTRIBUTION: Tropical Pacific and Indian oceans. SIZE: Up to 36 pounds (16.3 kg); most run about 4 to 5 pounds (1.8-2.3 kg). COLOR: Red above; silvery pink below; eye red and mouth red or pink; dorsal and tail fin red. □ In Hawaii caught over offshore drop offs, usually in water deeper than the uku or 'opakapaka at depths of 80 to 130 fathoms (146.3-237.7 m) but not more than 160 fathoms (292.6 m). This is also a common snapper taken over ledge areas and banks off Guam and Samoa, usually at depths of 100 fathoms (182.9 m) or more. Caught handlining year-round, mostly during daylight. Onaga is a very important market fish in Hawaii. The meat has a delicate sweet flavor and is usually served raw, "sashimi" style. It brings a high price at the market especially during the New Year's season when the demand for traditional "onaga-sashimi" is at its peak. Also prepared as a special dish for weddings.

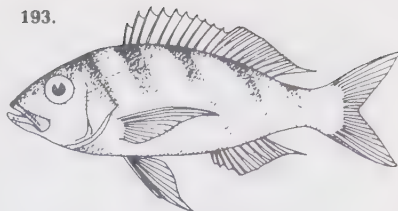
191. 'ULA'ULA (H), ehu (G), *Etelis marshi* (Jenkins). DISTRIBUTION: Tropical Indo-Pacific. SIZE: In Hawaii up to 2 feet (61 cm) long. In Guam this fish is known to reach 40 pounds (18.1 kg) in weight, but most caught are about 2 pounds (0.9 kg). COLOR: The 'ula'ula is similar in appearance and habits to the onaga, but lacks the red coloration on the inside of the mouth and usually has a yellowish band along the middle of the sides. □ Taken handlining along with onaga in Hawaiian waters, and one of the more common snappers found in Guam and American Samoa over offshore ledges and banks. An excellent food fish.

192.



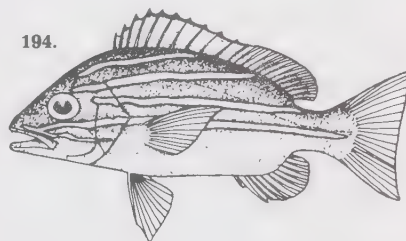
192. LEHI (G), *Aphareus rutilans* Cuvier and Valenciennes. DISTRIBUTION: Tropical Pacific. SIZE: Up to at least 3 feet (91 cm) long. COLOR: Brick red. □ A common Guam snapper taken handlining on the bottom over the Galvez Bank and off much of the leeward and windward coasts. This species also occurs in American Samoa and Hawaii, but is not important in the sport catch.

193.



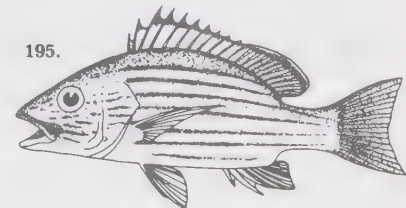
193. GINDAI (G), *Rooseveltia brighami* (Seale). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 20 inches (51 cm). COLOR: Alternating red and yellow vertical bars; dorsal, pectoral, and caudal fins yellow. □ This colorful Guam snapper is commonly taken over 100-fathom (182.9-m) drop offs around the island. It also occurs in American Samoa and occasionally appears in Hawaiian markets. A good food fish.

194.



194. TA'APE (H), savani (S), funai (G), bluelined snapper, yellow-and-blue seaperch, *Lutjanus kasmira* (Forskål). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Reported to reach 15 inches (38 cm) long. COLOR: Bright lemon yellow with pale-blue stripes edged with lavender or deep purple. □ This distinctively colored fish is probably the most abundant inshore snapper taken in American Samoa, where it is commonly found in water 20 to 100 fathoms (36.6-182.9 m) deep. Relatively common around Guam at depths of 35 to 40 fathoms (64.0-73.2 m), though generally incidental in the sport catch. Introduced to Hawaii from the Marquesas in 1958 and 1969, where it now has entered the sport and commercial catch in significant numbers. In the Hawaiian Islands ta'ape are found in large schools over hard bottom in water 40 to 100 feet (12.2-30.5 m) deep, with adults sometimes in water up to 240 feet (73.2 m) deep. Caught handlining at night; some are taken in traps in Hawaii. A very good food fish.

195.



195. TOAU (H), bua (G), red-margined seaperch, *Lutjanus fulvus* (Bloch and Schneider). DISTRIBUTION: Tropical Pacific. SIZE: Reaches a length of about 13 inches (33 cm). COLOR: Dusky yellow above fading to pale yellow or white below, with thin longitudinal yellow stripes along the sides.

the scale rows. Dorsal and tail fins dusky red; anal and pelvic fins yellow; pectoral fin yellow on upper edge; small gold flecks and broken lines on head and cheek area. □ An inshore fish found in brackish water and around stream mouths out to about 40 or 50 feet (12.2-15.2 m) of water, sometimes entering deep tide pools. Feeds on small fishes and invertebrates and often seen in small aggregations. Successfully introduced to Hawaiian waters in 1956 and 1958. Taken by hook and line from shore and from boats; taken also with gill nets, surround nets, and spears. Considered a very good food fish.

196.



196. KAKAKA (G), vava sui (S), feloitega (S), taiva uli'uli (S), *Lutjanus monostigmus* (Cuvier and Valenciennes). DISTRIBUTION: Tropical Pacific. SIZE: Up to 18 inches (46 cm); most caught are about 10-12 inches (25-30 cm). COLOR: Olive-green body (sometimes coppery red, particularly in Samoan waters); scales on side brassy; belly yellowish white or light coppery red; lips bright red; fins all bright orange yellow. In general, this fish usually is distinguished by the small but prominent black spot on its side. □ One of the larger nearshore snappers commonly taken from shore over reef areas around the island of Guam and American Samoa. Like some other members of the snapper family it has been linked with cases of ciguatera, or fish poisoning; but in Guam it is commonly eaten and is also sold in the markets of American Samoa despite reports of it sometimes being toxic there.

197.



197. MU (S), tagafi (G), *Lutjanus bohar* (Forskål). DISTRIBUTION: Widespread throughout the Tropical Pacific. SIZE: Attains 30 inches (76 cm). COLOR: Adult fish are uniformly red with a light greenish tinge around the head area; yellow eyes. Sometimes bronzy above, lighter below with two oval light spots on side. Base of pectoral and pelvic fins rosy; otherwise fins dusky. □ This snapper is commonly caught by handliners in American Samoa and Guam, usually in water 100 fathoms (182.9 m) or less, but does not occur in Hawaii. The flesh is reported to be poisonous and should not be eaten, even though in Guam many large fish (17-25 pounds or 7.7-11.3 kg), which are usually the most toxic, were taken by the Guam Division of Fish and Game in relatively deep water (35 fathoms or 64.0 m), and none proved to be poisonous.

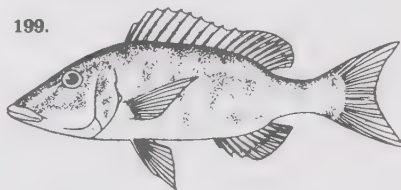
198.



198. MALA'I (S), fafaet (G), red snapper, *Lutjanus gibbus* (Forskål). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 24 inches (61 cm). COLOR: Body uniform red with red eyes. Large adults often are slightly dusky above and reddish below. □ A common snapper taken about reefs in American Samoa and Guam, occurring in moderately deep water. Usually taken handlining over the deeper parts of the reef; in Guam, some are taken spearing. Reportedly the flesh of this species causes severe poisoning in other parts of its range; however, fish taken from American Samoa and Guam waters are said to be not toxic and are commonly eaten.

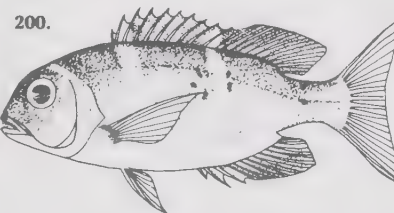
LETHRINIDAE: EMPERORS

199.



199. FILOA (S), lililok (G), green snapper, *Lethrinus miniatus* (Forster). DISTRIBUTION: Tropical Indo-Pacific and Red Sea. SIZE: Up to about 36 inches (91 cm). COLOR: Body dark brown to grayish, sometimes with dark mottling on sides; dorsal, anal, and tail fins pinkish; pectoral fin yellow. □ This long-snouted species is a common inshore reef fish in American Samoa and Guam, and is taken with a baited hook in water up to 100 feet (30.4 m) deep in American Samoa and up to 300 feet (91.4 m) in Guam. Large specimens are known to be slightly toxic in Samoa and other parts of this fish's range; however, it is said to be not toxic in Guam where it is highly prized as a food fish.

200.



200. MU (H), mamamu (H), mumu moaga (S), loalia (S), matanhagon (G), *Monotaxis grandoculis* (Forskål). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 2 feet (61 cm). COLOR: Dusky to olive green with two whitish crossbars (sometimes three and four bars); black crescent at base of pectoral. Dorsal fin brownish and reddish at tip; caudal and anal fins orange and yellow at base; anal, pectoral, and ventral fins reddish; inside of mouth red. □ This species occurs over reefs in Hawaii and is

common in Samoan waters. It is considered a good eating fish and is usually caught by handline. Some are taken with spears and nets.

MULLIDAE: GOATFISHES

201.



201. WEKE-'A'A (H), i'a sina (S), afolu (S), salmonete (G), spot weke, spot goatfish—young called "oama" in Hawaii and "teau" in Guam, *Mulloidichthys flavolineatus* (Lacépède). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 18 inches (46 cm); "oama" average about 5 inches (13 cm) or less. COLOR: Silvery white with a yellow horizontal band extending from eye to tail; spot as indicated. This fish can change its markings rather rapidly, with additional spots or blotches appearing along the lateral yellow band which becomes paler and edged with blue. □ A very common inshore goatfish throughout the Pacific Islands, occurring on or near the bottom in schools or small aggregations over sandy patches that intersperse reef areas. When feeding, it rummages in the sand for food with its fingerlike chin barbels, leaving puffs of sand clouds in its wake. In Hawaii during late summer the young or "oama" swarm in shallow sandy areas and are caught from shore with poles and lines. Adult fish are mostly speared or netted; some are caught in fish traps and handlining from boats. In Guam, juveniles (teau) are much sought after by cast netters and surround netters and are quite common in the lagoon habitat. Considered a good food fish.

202.



202. WEKE-'ULA (H), salmonete manining (G), vete (S), ula oa (S), red weke, red goatfish, *Mulloidichthys vanicolensis* (Cuvier and Valenciennes). DISTRIBUTION: Tropical Indo-Pacific and Red Sea. SIZE: Up to 16 inches (41 cm) long; usually about 8 to 10 inches (20-25 cm). COLOR: Rosy red on the dorsal region, fading to whitish pink below. There is a prominent light-yellow band along the sides, extending from the eye and fading out towards the tail region. Ventral and pectoral fins are pale rosy; caudal fin has a yellowish tinge. □ The weke-'ula is nocturnal, occurring in shallow-reef areas over sandy bottom, seeming to prefer more rocky surroundings than other goatfishes and deeper water of about 5 to 15 fathoms (9.1-27.4 m); probably deeper off the Kona coast of Hawaii. In Hawaii the weke-'ula is

usually netted, although sometimes taken by hook and line from shore and from boats or by "torch fishing" with spears or hand nets. A good food fish.

203. MALU (H), salmonete acho (G), goatfish, *Parupeneus pleurostigma* (Bennett). DISTRIBUTION: Widespread in the central Indo-Pacific. SIZE: Reaches a length of about 16 inches (41 cm). □ This is another relatively common goatfish similar to the weke-a'a in habits and appearance, except the malu is stockier, the base of the soft-rayed dorsal fin is very dark, and the blotch on the side is more deep than long. Taken by spearing and with nets.



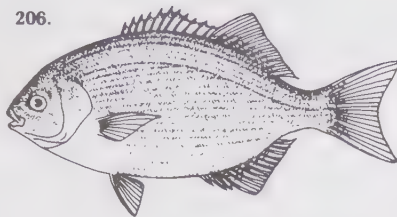
204. KUMU (H), red goatfish, *Parupeneus porphyreus* (Jenkins). DISTRIBUTION: Tropical Pacific. SIZE: Up to 8 or 9 pounds (3.6-4.1 kg); usually 1 to 3 pounds (0.5-1.4 kg). COLOR: Usually reddish with a rather prominent stripe through the eye, although young specimens occasionally have a greenish-color phase. Distinguished by the white saddle behind the soft dorsal fin. □ A fairly common Hawaiian goatfish found at various depths throughout reef areas especially under coral heads, often coming very close to shore. Caught mostly by spearing and in traps during the day; some are taken at night by spears of divers or waders on the reef with lights. The kumu is an extremely prized food fish in Hawaii. The flesh is considered a delicacy.



205. MOANO (H), *Parupeneus multifasciatus* (Quoy and Gaimard). DISTRIBUTION: Hawaiian Islands. SIZE: Up to 12 inches (30 cm) or so; averages about one-third of a pound (less than 0.2 kg). COLOR: Dark red with alternating bands of pale rosy red and darker red. Usually distinguished by the dark-red-to-black bar that extends down between the two dorsal fins. □ This small goatfish is found over sand bottom from the shore to depths of about 40 fathoms (73.2 m), and like the other goatfishes mentioned it is usually found where patches of sand intersperse rock or coral. An abundant inshore reef fish, taken in traps and by shore anglers with spinning and bait-casting gear, often along with papio and other small goatfishes. On the big island of Hawaii most are speared, though some are taken handlining (drifting and at anchor). Although small, the moano is considered by some to be among the tastiest of Hawaiian food fishes.

KYPHOSIDAE: RUDDERFISHES, SEA CHUBS

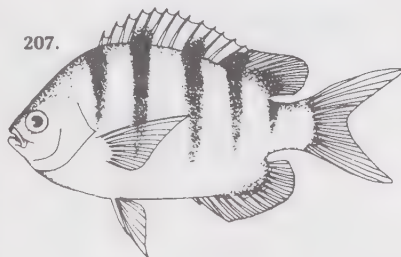
206.



206. NENUE (H), manaloa (H), nenu parii (H), guili (G), sea chub, rudderfish, *Kyphosus cinerascens* Forskål. DISTRIBUTION: Tropical Indo-Pacific and Red Sea. SIZE: Up to 10 or 12 pounds (4.5-5.4 kg); averages about 4 to 6 pounds (1.8-2.7 kg). COLOR: Gray brown with blue reflections, lighter below. Narrow dark bands on sides between scale rows. Some fish have irregular blotches of yellow on sides, and on rare occasions a specimen may be entirely yellow. □ In Hawaii, the nenu is partial to rough and turbulent waters along rocky coasts where it is often found in large schools. In Guam, it seems to prefer the edges of channels and reef margins. This species feeds mostly on algae. Large fish are generally taken by spear, cast nets, and gill nets; the young are sometimes caught during the day by hook and line. Nenu is rather difficult to hook because of its small mouth, but when hooked it fights vigorously. Generally not esteemed as a food fish in Hawaii, but some consider it a delicacy—it is much sought after by Guamanians. The flesh has a strong flavor, probably due to the fish's algal diet.

POMACENTRIDAE: DAMSELFISHES

207.

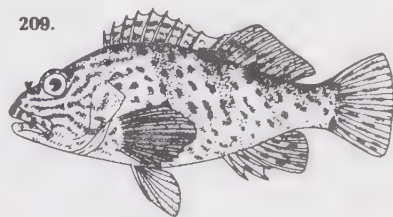


207. MAOMAO or "mamo" (H), *Abudefduf abdominalis* (Quoy and Gaimard). DISTRIBUTION: Hawaiian Islands. SIZE: Up to 9 inches (23 cm); most taken are about 5 inches (13 cm) long. COLOR: Pale brassy or green with four or five black vertical bars as indicated. Belly white with yellow tinge near the anal fin. □ This delicious little pan fish abounds in shallow-water reefs, harbors, and bays throughout the islands. It feeds on small crustaceans in the water and is often found in loose aggregations hovering over the reef or darting around pilings and other underwater structures. Maomao are the prime quarry of Hawaii's children who catch them from shore with pole and line using a very small hook. Also caught by spearing, in traps, and with cast nets.

208. KUPIPI (H), dodo (G), sergeant major, *Abudefduf sordidus* (Forskål). □ This fish is similar in appearance and habits to maomao, but is readily distinguished from it by a prominent black spot near the tail immediately behind the soft dorsal fin. The body color is also more grayish than that of maomao.

CIRRHITIDAE: HAWKFISHES

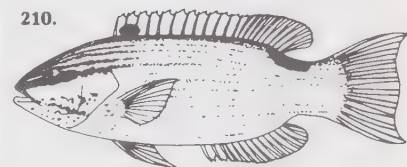
209.



209. PO'O-PA'A (H), 'o'opu-kai (H), spotted hawkfish, *Cirrhitus pinnulatus* (Bloch and Schneider). DISTRIBUTION: Tropical Pacific. SIZE: Up to about 10 inches (25 cm); most caught are about 5 inches (13 cm) long. COLOR: Red, brown, and white spottings and mottlings. □ Like the rest of the hawkfish family this fish is characterized by a fleshy fringe on the snout. This nocturnal predator prefers the turbulent water of the surge zone where it lies in wait for passing prey, sometimes on large rocks or coral heads. Occasionally it darts out to snatch its prey, then returns to its original post or swims to another vantage point to begin another vigil. During the day, the po'o-pa'a hides in crevices in the reef. Taken by hook and line and spearing. Considered only fair as a food fish, and is used mainly in making soup. The meat tends to fall apart when fried.

LABRIDAE: WRASSES

210.



210. 'A'AWA (H), hinalea (H), spot wrasse, blackspot wrasse, *Bodianus bilunulatus* (Lacépède). DISTRIBUTION: Tropical Pacific. SIZE: Up to about 24 inches (61 cm) or about 8 or 9 pounds (3.6-4.1 kg); most caught are about 5 pounds (2.3 kg) or under. COLOR: Highly variable with age and sex as is the case with many members of the wrasse family. Females go through three color phases with growth: fish 4 to 12 inches (10-30 cm) long are nearly all red with a black spot under the soft dorsal fin; those over 12 inches (30 cm) are usually plain bluish black. Males are marked as illustrated; dark reddish brown or purplish bands on head area thinning to narrower and somewhat redder stripes on sides and belly, which is white or pale yellow; eye red; pronounced white band on head area; dorsal, caudal, and anal fins yellow. □ The 'a'awa is one of the larger Hawaiian wrasses and is fairly abundant throughout the coral reef habitat. It is

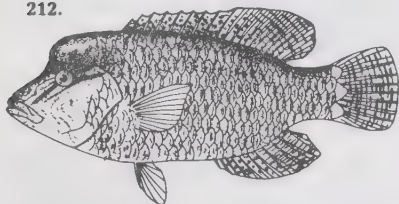
taken on the bottom in shallow water out to depths of about 100 feet (30.5 m) or more, with bigger fish occurring in deeper water. The 'a'awa, like other members of the wrasse family, is active during the day and hides among coral or under sand at night. Caught handlining from boats, usually while fishing for other species and often considered a nuisance. Sometimes taken by spear. Opinions on the food value of this fish vary from poor to good.

211.



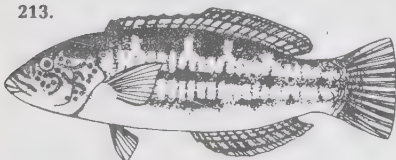
211. PO'OU (H), *Cheilinus rhodochrous* Günther. DISTRIBUTION: Tropical Indo-Pacific. SIZE: Up to 2 feet (61 cm); most are about 10 inches (25 cm) or about $\frac{3}{4}$ pound (0.3 kg). COLOR: Highly variable with growth. At 10 inches (25 cm), plain olive drab with a white saddle near the tail (see illustration). Fish 20 inches (51 cm) and over have no white saddle, but have large black spots at base of the dorsal and anal fins, and the ventral fin is dark. □ The po'ou is commonly found in reef areas around the islands of Molokai, Lanai, Maui, and Hawaii, at depths up to 40 or 50 feet (12.2-15.2 m). In the Hawaiian Islands it is often caught along with 'a'awa' while handlining and spearing. Taken by spear in Guam. A good food fish.

212.



212. TANGISUN (G), *Cheilinus undulatus* Rüppell. DISTRIBUTION: Tropical Indo-Pacific. SIZE: Known to reach 5 to 6 feet (152-183 cm) or more in length, and over 100 pounds (45.4 kg). COLOR: Mostly a dull, mottled olive green, each scale with a vertical purplish line; red and green bars and spots on dorsal and anal fins; tail fin edged with yellow; pelvic fins yellow. □ This exceptionally large wrasse is caught in Guam; however, large specimens frequently taken by local anglers before the advent of scuba are now much less common. This humpheaded wrasse is much prized and an excellent food fish. Taken spearing and sometimes bait casting.

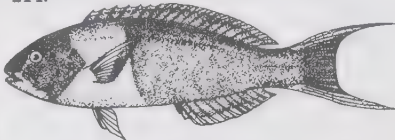
213.



213. HINALEA (H), aaga (G), *Thalassoma fuscum* (Lacépède). DISTRIBUTION: Tropical Pacific. SIZE: Up to 11 inches (28

cm); usually about 6 inches (15 cm). COLOR: Pale greenish with two or three irregular, broad, horizontal rosy stripes, which intermingle with greenish stripes, brown blotches, and purplish bars. Dark-brown-to-black spots and reticulations on head. □ This colorful wrasse is common to open rocky surge areas and shallow-water coral reefs, and is sometimes found in deepwater tide pools. Although principally a daytime feeder, the hinalea is often taken at night and is caught by hook and line from shore as well as from boats in the Hawaiian Islands. It is taken occasionally by spear in Guam. The very slimy skin makes it difficult to hold. Opinions vary on its food value; generally not sought after.

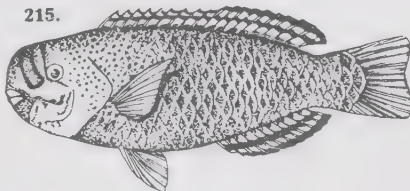
214.



214. HINALEA LAUWILI (H), 'a'ala'ihī (H), saddle wrasse, *Thalassoma duperreyi* (Quoy and Gaimard). DISTRIBUTION: Hawaiian Islands. SIZE: Up to about 12 inches (30 cm); most caught are under 6 inches (15 cm). COLOR: Adults are green with a striking orange-brown shoulder bar. □ A very abundant Hawaiian wrasse found throughout the islands along shallow rocky shorelines as well as in pure reef areas. This fish has an annoying habit of robbing a baited hook meant for more desirable species and is often considered a pest by anglers seeking bigger and tastier game; its food value is considered poor.

SCARIDAE: PARROTFISHES

215.



215. UHU (H), green parrotfish, *Scarus perspicillatus* Steindachner. DISTRIBUTION: Hawaiian Islands. SIZE: Up to 2 feet (61 cm) or more; most caught are around 14 inches (36 cm) long. COLOR: Males and females differ markedly and were once thought to be two separate species. Large males have a distinctive dark band that extends down below the eye across a humplike snout. The body is olive colored, with each large scale edged with yellow. The dorsal fin is pea green with black stripes and peacock blue at the base. Chin area, edge of tail, ventral fin, are also a vivid peacock blue. Females are reddish brown with red fins, and the head profile is gently sloping, not vertical as in the adult male. □ Found in rocky areas and coral reefs, usually more abundant at the reef's outer edges in water 2 to 4 fathoms (3.7-7.3 m) and deeper. Like other members of the parrotfish family, it scrapes algae off the surfaces of rocks and dead coral with its beaklike jaw teeth during the day, resting

amid rock and coral at night. Young fish sometimes secrete a mucous envelope about themselves during the night which presumably serves as protection against predators. It is the largest and most commonly speared parrotfish in Hawaiian waters—and the most prized. An excellent food fish.

216. UHU (H), parrotfish, *Scarus dubius* Bennett. □ Another common parrotfish taken by spear in Hawaii. Primarily bright orange with blue markings. Attains a length of about 14 inches (36 cm).

217. HUMPBACK PARROTFISH, *Scarus gibbus* Rüppell and *Cetoscarus bicolor* (Rüppell). □ These two parrotfishes are highly sought by Guam anglers. Not as common as they once were, especially the large specimens; both are hunted with spears. *S. gibbus*, larger of the two, is known to reach 30 to 40 pounds (13.6-18.1 kg). Food value is excellent.

MUGILIDAE: MULLET

218.



218. 'AMA'AMA (H), aguas (< 8 in., G), liguan (> 8 in., G), striped mullet, mullet, *Mugil cephalus* Linnaeus. DISTRIBUTION: Tropical and temperate seas, worldwide. SIZE: Up to about 18 inches (46 cm); most caught are around 12 inches (30 cm) long. COLOR: Silvery gray. □ Although schools of 'ama'ama are found along the open coast, they seem to prefer calm waters close to shore, around mouths of streams and inlets and in brackish-water bays and harbors. Just about the most difficult fish to catch by pole and line, but this does not seem to discourage a select breed of Hawaiian islanders who patiently wait for this finicky fish to take a tiny hook baited with bread or limu (seaweed). For those with less patience, the 'ama'ama can be taken by a variety of other fishing gear such as cast nets, gill nets, and surround net (hukilau) and at nighttime torchlight fishing with hand nets or cast nets. In Hawaii the fishing season is closed December through February. On American Samoa this fish is taken mostly with cast nets, and in Guam most are taken with cast nets and surround nets, although light spinning tackle is sometimes used near sand beaches. An important food fish. In Hawaii a small number are raised commercially in fish ponds.

219.



219. UOUOA (H), false mullet, *Neomyxus leuciscus* (Günther). DISTRIBUTION: Tropical Pacific. SIZE: Up to 18 inches (46

cm); usually 6 inches (15 cm). **COLOR:** Silvery with a yellow mark on the upper part of the pectoral fin. □ The uouoa (often pronounced wo-wo) occurs along sandy shores and in tide pools as well as in rocky surge areas. Common throughout the Hawaiian Islands, where most are taken with cast nets, some by hook and line using bread for bait. This species also occurs in Guam, but is not common. A good food fish.

SPHYRAENIDAE: BARRACUDAS

220.



220. **KAKU** (H), alu (G), great barracuda, *Sphyræna barracuda* (Walbaum). **DISTRIBUTION:** Tropical seas and Atlantic and Pacific oceans. **SIZE:** All-tackle record (Lagos, Nigeria) is 83 pounds (37.6 kg) with a length of 6 feet ¼ inch (183.6 cm). Most caught by anglers are under 50 pounds (22.7 kg), average is 5 to 10 pounds (2.3-4.5 kg). **COLOR:** Slate colored dorsally turning silvery on sides and belly. Black flecks on sides. □ The kaku occurs inshore as well as offshore and in a variety of habitats. Young fish frequent brackish-water areas and sometimes enter drainage ditches and fish ponds in the Hawaiian Islands. When close to shore in bays or around stream mouths barracuda are usually solitary, but offshore this species tends to travel in schools or small aggregations. Caught casting from shore and trolling lures and baits and handlining from boats. A wire leader is essential. This aggressive and toothsome predator should be regarded with caution, in and out of the water. Considered only fair as a food fish.

The kawalea, or Japanese barracuda (*Sphyræna helleri* Jenkins), is another species of barracuda taken by anglers and is usually caught handlining. It is a much smaller fish than the kaku, and reaches a length of about 2 feet (61.0 cm). A similar species, *Sphyræna forsteri*, occurs in Samoa and Guam waters, known locally as "sapatu" and "alu," respectively.

POLYNEMIDAE: THREADFINS

221.



221. **MOI** (H), young called "moi-li'i" (H), boca dulce (G), Pacific threadfin, *Polydactylus sexfilis* (Cuvier and Valenciennes). **DISTRIBUTION:** Tropical Indo-Pacific. **SIZE:** Reportedly reaches about 24 inches (61 cm) long and about 10 pounds (4.5 kg); most caught are about 12 to 14 inches (30-36 cm). **COLOR:** Dusky above, silvery on sides and belly; fins black-tipped. □ The moi is a highly sought-after food and game fish in Hawaii, where it is found in sandy holes (called "moi holes") along rocky shores, and along sandy

beaches in surge areas. From August through December small moi or "moi-li'i" occur in large schools along beaches and in sheltered coves with some venturing into tide pools. Primarily taken casting with baits, plugs, and spoons; also taken with cast nets, gill nets, and spears. Moonlit nights are considered best for catching moi by casting, although this popular sport fish is caught both night and day.

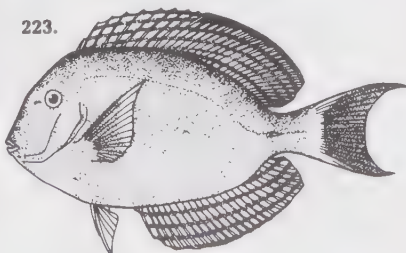
ACANTHURIDAE: SURGEONFISHES

222.



222. **MANINI** (H), kicho (G), convict tang, *Acanthurus sandvicensis* Streets. **DISTRIBUTION:** Widespread throughout the tropical Indo-Pacific. **SIZE:** Up to 9 inches (23 cm); averages about 6 inches (15 cm). **COLOR:** Silvery, sometimes with a yellowish tinge; black vertical bars. □ This is Hawaii's most abundant surgeonfish and can be found in almost any reef area throughout the islands in both calm and turbulent water. It is also common about Guam. The young inhabit tide pools, but with maturity work their way into deeper water. Primarily a schooling fish, but can also be seen singly or in small aggregations. In Hawaii the manini is usually taken by cast nets, but some are also taken with pole and line using shrimp or a special blend of octopus ink (each angler has his own recipe) as well as with gill nets, traps, and spears. In Guam, most are taken with nets and spears. An excellent food fish.

223.

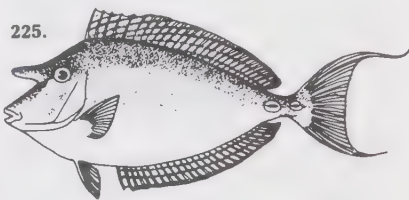


223. **PUALU** (H), ugupao (G), *Acanthurus xanthopterus* Cuvier and Valenciennes. **DISTRIBUTION:** Tropical Indo-Pacific. **SIZE:** Up to about 20 inches (51 cm); usually about 10 inches (25 cm) long. **COLOR:** Uniform purplish gray, sometimes with irregular dark stripes along sides; dorsal and anal fins with three or four longitudinal blue bands. □ The pualu is found in bays and harbors as well as in deep outer reefs where coral is interspersed with sand; usually at depths of 30 feet (9.1 m) or more. Taken with pole and line; also trapped, netted, and speared. Like most surgeonfish, the pualu should be

handled with respect. It carries formidable weapons at the base of the tail in the form of recurved spines which it can erect by bending its caudal peduncle, and it usually does so when threatened. These bladelike spines can inflict a nasty wound. Opinions on its food value vary from fair to good.

224. **PALANI** (H), ugupao (G), surgeonfish, *Acanthurus dussumieri* Cuvier and Valenciennes. **DISTRIBUTION:** Tropical Indo-Pacific. **SIZE:** Up to and exceeding 18 inches (46 cm). **COLOR:** Spotted with black; bright-blue tail fin; fine blue lines on body fading towards belly; caudal spine white and broadly edged with black; yellow dorsal and anal fin. □ The palani, a close relative of the pualu, is another surgeonfish that occasionally enters the sport catch in Hawaii and Guam. It occurs in bays and outer reef areas over sandy patches. Most are taken by traps; some are speared. Food value considered fair.

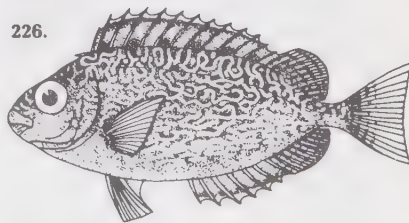
225.



225. **KALA** (H), tataga (G), ume (S), ili'ilia segi (S), unicornfish, *Naso unicornis* (Forsk.). **DISTRIBUTION:** Tropical Indo-Pacific. **SIZE:** Reaches a length of 24 inches (61 cm); averages about 16 inches (41 cm) long. **COLOR:** Dusky olive; fins light blue; also light blue around the double keel blades. Body color is sometimes very pale. □ The kala occurs in inshore reef areas and along rocky shores where it feeds on algae. It is a schooling fish; however, large individuals are sometimes seen singly on the outer edges of the reef. The young are found occasionally in tide pools. Characterized by the horn on its snout just about at eye level, which is hardly noticeable in young specimens, but lengthens with age. The skin is leathery and strong, and the two keel blades on each side of the tail are immovable and always in an open position. In Hawaii, kala are mostly speared, although some are taken with cast nets, gill nets, and hooks and lines. In Guam, this fish is taken spinfishing and with surround nets. Food value considered only fair.

SIGANIDAE: RABBITFISHES

226.



226. **SESJUN** (G), rabbitfish, *Siganus spinus* (Linnaeus). **DISTRIBUTION:** Tropical Indo-Pacific. **SIZE:** Most caught in Guam are 8 or 9 inches (20-23 cm) in length. **COLOR:** Brown with narrow bluish lines forming a reticulated pattern along

the back; head plain gray or brownish; cheeks silvery; tail fin with three to four faint brown bars. Has slimy slippery skin with tiny concealed scales. □ *Sesjun* is a herbivorous species that browses across rock or reef areas, often in large schools. It is a very common shallow-water reef fish found around the island of Guam, where it is caught with cast nets, gill nets, and surround nets. This fish should be handled carefully—it can inflict venomous puncture wounds with its fin spines. An excellent food fish.

SCOMBRIDAE: MACKERELS AND TUNAS

227.



227. 'AHI (H), asi (S), yellowfin tuna, *Thunnus albacares* (Bonnaterre). DISTRIBUTION: Cosmopolitan in tropical and subtropical seas. SIZE: All-tackle record (San Benedicto Island, Mexico) is 308 pounds (139.8 kg) with a length of 7 feet (213.4 cm). In Hawaii, fish are known to range up to 300 pounds (136.1 kg); average size varies with fishing area. In general, deepwater fish found at about 1,000 fathoms (1,828.8 m) averaged about 100 pounds (45.4 kg); those caught in 25 to 100 fathoms (45.7-182.9 m) averaged about 20 pounds (9.1 kg). COLOR: Blue green above, white below. A faint yellow stripe that fades after death, extends from eye to tail. Soft dorsal and anal fins and finlets bright yellow; the dorsal and anal fins lengthen with age. □ 'Ahi is a pelagic schooling fish found over deepwater banks and submarine ledge areas. The young often travel near the surface feeding on schools of bait fishes and squid. This popular game fish can be caught year-round throughout the Pacific Islands, trolling or handlining with feathered jigs, plugs, or spoons. In Hawaii, most fishing takes place July to November; in Guam, February to August; and in American Samoa, March to July. Excellent eating, cooked or raw (sashimi style).

228.



228. KAWAKAWA (H), black skipjack tuna (G), little tunny, bonito, false albacore, *Euthynnus affinis* (Cantor). DISTRIBUTION: Indo-Pacific. SIZE: Up to about 20 pounds (9.1 kg); most caught are around 4 or 5 pounds (1.8-2.3 kg). COLOR: Dark green or blue above, silvery below; dark wavy marks on dorsal area as indicated; one to five dusky spots below pectoral fin are usually present. □ The kawakawa is a schooling pelagic species usually caught trolling over 100-fathom (182.8-m) drop offs, and often in association with aku,

skipjack tuna. Present in Hawaiian waters throughout the year, but most abundant during summer when the fish come fairly close to shore in large schools. In Guam they appear to be most abundant in early spring. Anglers are guided by seabirds that follow the schools and feed on small fishes that the kawakawa flush to the surface. A hard-fighting game fish. Good eating, although not as much in demand as some of the other tuna species.

229.



229. AKU (H), atu (S), skipjack tuna, bonito, *Katsuwonus pelamis* (Linnaeus). DISTRIBUTION: Cosmopolitan in temperate and tropical seas. SIZE: All-tackle record in the Indian Ocean (Baie du Tambeau, Mauritius) is 40 pounds (18.1 kg) with a length of 38 3/4 inches (98.4 cm). In Hawaii, aku average about 18 to 22 pounds (8.2-10.0 kg) in summer; 5 to 12 pounds (2.3-5.4 kg) rest of year. In Guam, this fish usually runs 3 to 7 pounds (1.4-3.2 kg) most of the year; 10 to 12 pounds (4.5-5.4 kg) seasonally. COLOR: When alive, dark metallic blue above, light dusky blue below, dark stripes as indicated. Latter half of dorsal region bright blue with oblique purplish stripes which fade soon after death. When excited or feeding, broad dusky bars sometimes appear on sides. □ The aku is a schooling, pelagic species common throughout the Pacific Islands, its habits being generally the same as the kawakawa's. Sometimes in certain areas such as off southeastern Lanai, aku come relatively close to shore; more often they are found in water 100 fathoms (182.9 m) and deeper. Caught trolling year-round using feathered jigs and other small lures, and located by flocks of seabirds. Best fishing in Hawaii is in summer; in American Samoa from about October to March; and in Guam from February to August. The fish has excellent flavor; is popular for sashimi and dried. Also used as bait for marlin.

230.



230. TAGI (S), dogtooth tuna, scaleless tuna, white tuna, *Gymnosarda unicolor* (Rüppell). DISTRIBUTION: Tropical Indo-Pacific. SIZE: Reported to reach 250 pounds (113.4 kg), but averages about 20 pounds (9.1 kg). COLOR: Deep purple above, silvery below; finlets yellowish. □ Tagi is a migratory fish found along the edges of deepwater reefs and submarine ledges where the bottom abruptly drops off into deeper water. It either schools in small groups or is solitary. This fish is not as deep bodied as other members of the tuna family and is distinguished by its large "peglike" teeth and lack of body scales. A fine food and game fish that puts up a hard, jerky fight when hooked. Caught

trolling and also drifting with live, cut, whole baits. In American Samoa the dogtooth tuna is commonly taken handlining at dusk and at night over 100-fathom (182.8-m) drop offs. Caught only incidentally around Guam and does not occur in Hawaii.

231.



231. ONO (H), tosun (G), wahoo, *Acanthocybium solandri* (Cuvier and Valenciennes). DISTRIBUTION: Tropical Atlantic and Pacific oceans. SIZE: All-tackle record (Cat Cay, Bahamas) is 149 pounds (67.6 kg) with a length of 6 feet 7 3/4 inches (202.6 cm). In Hawaiian and Samoan waters, ono average around 30 to 40 pounds (13.6-18.1 kg). In Guam, tosun, average about 20 pounds (9.1 kg). COLOR: Generally dark blue above fading into silvery below with about 30 purplish-gray bars on sides that flash bright blue when the fish is fighting a hook. □ Ordinarily a solitary fish that roams the surface waters of the open sea, usually over deep-sea ledges where the bottom drops off sharply. Often seen near floating logs and other debris that provide shelter to small fish upon which the ono feeds. In Hawaii ono are often caught along with 'ahi while trolling over submarine ledges in water 25 to 100 fathoms (45.7-182.9 m) deep. Taken intermittently throughout the year over the billfish grounds off Guam. In American Samoa caught trolling along nearshore 100-fathom (182.9-m) drop offs as well as offshore. The ono is a strong persistent fighter. Its pointed jaws studded with sharp teeth should be carefully avoided. An excellent food fish; aptly named "ono," Hawaiian word meaning "to have sweet taste."

XIPHIIDAE: SWORDFISHES

232.



232. A'U (H), mekajiki (H), swordfish, broadbill, *Xiphias gladius* (Linnaeus). DISTRIBUTION: Cosmopolitan in tropical and temperate seas. SIZE: All-tackle record (Iquique, Chile) is 1,182 pounds (536.2 kg) with a length of 14 feet 1 1/4 inches (455.4 cm). Averages about 250 pounds (113.4 kg) in Hawaii's commercial catch. COLOR: Varies from metallic purplish to blackish brown to almost black; generally, dark brown. □ This solitary open-ocean fish is sought by big-game anglers throughout its range but few are ever taken by them in the tropical Pacific. Broadbill are hard to find, hard to hook, and even harder to land. In Hawaii, most are taken by commercial longliners. Sport-caught fish are usually taken slow-trolling or drifting live, whole, and cut baits. Distinguished from the marlins by a sword that is flattened rather than rounded in cross section, and by the rigid dorsal fin that is not retractable as in other billfishes. An excellent food fish.

ISTIOPHORIDAE: BILLFISHES

233.



233. A'U'LEPE (H), bashokajiki (H), saula-lele (S), sailfish, *Istiophorus platypterus* (Shaw and Nodder). **DISTRIBUTION:** Cosmopolitan in tropical seas. **SIZE:** All-tackle record in the Pacific (Santa Cruz Island, Galapagos) is 221 pounds (100.2 kg) with a length of 129 inches (327.7 cm). In the Pacific Islands sailfish average about 50 pounds (22.7 kg) or less. **COLOR:** Sail cobalt blue to purple; body dark steely blue above and silvery white below; sides with pale-purple vertical bars. □ A pelagic open-ocean fish, often solitary, but known also to occur in small schools or groups, preferring warm-water temperatures between 74° to 88°F. One of the leading game fishes in American Samoa, where it is taken surface trolling with baits and lures year-round. Also taken by sportsmen over the billfish grounds off Guam. Relatively rare in Hawaiian waters, and only occasionally taken by anglers—most are caught by commercial longliners. When swimming, the huge saillike dorsal fin folds into a fleshy groove at its base, but often is raised when the fish is fighting a hook. Its food value is poor, although some fish are smoked.

234.



234. A'U (H), shirokajiki (H), black marlin, *Makaira indica* (Cuvier and Valenciennes). **DISTRIBUTION:** Tropical and temperate Pacific and Indian oceans. **SIZE:** All-tackle record (Cabo Blanco, Peru) is 1,560 pounds (707.6 kg) with a length of 14½ feet (442.1 cm). Known to reach 1,800 pounds (816.5 kg); averages about 200 pounds (90.7 kg). **COLOR:** Variable. Most are dark slate blue above, silvery below lateral line. Sometimes a fish may have pale-blue stripes or blue patches on sides that fade quickly after death. □ The black marlin is the largest of all game fishes and highly prized by blue-water anglers, although only occasionally taken around the Hawaiian Islands and off Guam and rarely taken in American Samoa. It is an open-ocean fish and usually solitary. Distinguished from all other billfishes by the rigid pectoral fin that cannot be folded against the body without breaking the joint. It is also wider and deeper around the head than all other billfishes. Caught slow trolling with baits, fast trolling with lures; also drifting and at anchor with fresh or live baits. In Hawaii, the chance of landing one is best while trolling off the Kona coast or off Kauai.

235.



235. A'U (H), kurokajiki (H), saula (S), blue marlin, *Makaira nigricans* Lacépède. **DISTRIBUTION:** Tropical and temperate waters of the Indo-Pacific and Atlantic oceans. **SIZE:** All-tackle record (Ritidian Point, Guam) is 1,153 pounds (523.0 kg) with a length of 14 feet 8 inches (447.1 cm); however, an unofficial catch was recorded at over 1,600 pounds (725.8 kg) from off Oahu. In the Pacific Islands, most run about 300 or 400 pounds (136.1-181.4 kg). **COLOR:** When alive, cobalt blue above and silver below; sometimes with pale-blue stripes on sides and blue patches on dorsal area and tail. Colors fade quickly after death and fish becomes a dark slate blue. □ Occasionally confused with the striped marlin, but distinguished by its more robust form and relatively low dorsal fin, of which the longest fin rays are shorter than the greatest depth of the body. Differs from the black marlin in that the pectoral fin can be folded flush to the sides of the body. The blue marlin is the most tropical of marlins, usually occurring in water 70° to 88°F. It is the leading big game fish in the central Pacific and the most abundant sport-caught marlin in Hawaii, American Samoa, and Guam. This extremely powerful and fast-swimming fish feeds mainly on members of the tuna family, particularly the skipjack tuna or aku. Occurs year-round throughout the islands covered here, and in Hawaii is most abundant during the summer. Sport fishing boats troll over bank areas looking for signs of schooling baitfish upon which marlin feed, or troll over offshore ledges where the bottom drops precipitously from 100 to 1,000 fathoms (182.9-1,828.8 m) or more. Trolling with large Hawaiian lures or "konaheads" is especially productive, although live, cut, and artificial baits also are used.

236.



236. A'U (H), naraigi (H), makajiki (H), striped marlin, *Tetrapturus audax* (Philippi). **DISTRIBUTION:** Temperate and tropical waters of the Indo-Pacific. **SIZE:** All-tackle record (Cape Brett, New Zealand) is 415 pounds (188.2 kg) with a

length of 11 feet (335.4 cm). Hawaiian striped marlin may reach up to 150 pounds (68.0 kg), but rarely over 100 pounds (45.4 kg), usually about 80 to 90 pounds (36.3-40.8 kg). **COLOR:** Royal blue above, silvery below; lavender or pale-blue stripes; dorsal and anal fins cobalt blue. These colors are most vivid when the fish is striking or fighting the hook. □ Of the island groups discussed here, this species occurs only in Hawaii, where it is relatively common and the leading billfish taken commercially. It is not, however, caught by sport anglers in as many numbers as the blue marlin, probably because most recreational fishing for billfish in Hawaii occurs during the summer, a time of year when striped marlin are least abundant according to commercial catch records (striped marlin catches tend to peak in spring and fall with few taken during the summer; the largest fish are taken in the fall). It is a beautiful fish and the most acrobatic of the marlins, often making breathtaking leaps into the air in its struggle to free itself from the hook. Usually caught slow trolling with live baits. It is more slender than the blue or hefty black marlin and is distinguished by the high pointed dorsal fin, the first rays of which are higher than the greatest depth of the body, and a greater number of stripes on the body than the blue marlin. A high-priced food fish in Hawaii, popular for sashimi and smoked.

SCORPAENIDAE: SCORPIONFISHES

237.



237. NOHU (H), nohu omakaha (H), scorpionfish, *Scorpaenopsis cacopsis* Jenkins. **DISTRIBUTION:** Hawaiian Islands. **SIZE:** Up to at least 20 inches (51 cm). **COLOR:** Mottled reddish. □ The nohu is usually found on the outer edges of reefs in water over 20 feet (6.1 m) deep. This fish lives on the bottom where it blends in remarkably well with its surroundings, often making short lunges to capture unsuspecting prey. Although it resembles the highly venomous stonefish of the tropical Pacific, there have been no reports of injuries from being spined by the nohu. Taken handlining and by spearing, also in traps. Highly regarded as a food fish.

Glossary of Terms

A-FRAME NET A one-man net fitted on a 6-foot long 'A' frame, used to capture smelt (family *Osmeridae*) as the fish come inshore to spawn in the surf. The net is held near the pointed end of the "A" and planted down barrierlike in the surf, facing the beach. The fish are caught as they ride the backwash out to sea and are shoveled into the wide end of the net, then shaken back into a sack at the pointed end. (See also **SURF NETTING**.)

ANADROMOUS Refers to fishes that spend most of their lives in salt and brackish waters but ascend rivers to spawn in fresh or nearly fresh water.

BOTTOMFISHING Fishing a bait or lure on or near the bottom from an anchored or drifting vessel. The bait is usually weighted and allowed to remain stationary until a fish bites or the angler retrieves it.

CASTING Throwing forth a bait or lure, letting out line at each throw and then retrieving it. The bait also can be allowed to sink to the bottom or drift with the current.

CAST NET A one-man circular net weighted at the rim with small sinkers and designed to be flung over the water so that it falls face down or dishlike over schools of fishes, entrapping them as it sinks to the bottom. Also called throw net and hand casting net.

CHARTER BOAT A fishing boat hired for the exclusive use of one or more anglers, usually for a particular type of fishing. Tackle and bait usually are furnished.

CHUMMING A means of attracting fish to the hook by throwing whole or chopped fish or shellfish into the water. Oily fish usually make the best chum. In some areas bread crumbs and corn meal are also used as chum. Live bait chumming is allowed in some areas, prohibited in others.

CIGUATERA An illness with symptoms such as diarrhea and paralysis caused by eating certain fishes living in tropical and subtropical regions, usually where coral reefs are well developed. It is seldom fatal.

COASTAL Refers to marine fishes which spend much of their lives within a few miles of shore.

CONTINENTAL SHELF A submarine plain extending out from shore to a depth of 100 fathoms (183 meters),

beyond which the ocean bottom begins a relatively rapid descent to the deep ocean floor.

CRAB RING A crab trap made of coarse mesh webbing attached to two iron hoops, designed to lie flat on the bottom but form a basket when raised. A bag of small mesh netting containing bait (scrap fish or shellfish) is secured to the center of the smaller inner ring to attract the crab and keep it occupied while the trap is pulled out of the water. Popularly used for market (Dungeness) and rock crab along the coast from central California north to Oregon and Washington.

DIP NET A conical small-mesh net attached to a rigid frame on a long handle and used to catch fish and other marine animals. Also called a hand net or scoop net.

DRIFT FISHING Trailing a weighted or unweighted line with live or dead baits behind a drifting boat. Artificial lures are sometimes used, particularly when "jigging."

ESTUARY A partially enclosed body of water having a free connection with the open sea; within it saltwater and freshwater mix.

FEEDER SALMON A term usually applied to smaller, sexually immature salmon that concentrate in an area to feed, opposed to large, mature salmon that move into an area prior to spawning.

FISH TRAP A portable trap for fish and shellfish usually made of wire mesh fitted over a rigid frame with an opening on one side. Like all traps it is designed so that entry is easier than exit. In the tropical islands fish traps are commonly used to capture a variety of reef animals.

GILL NET A curtainlike net suspended in the water with mesh openings large enough to permit only the heads of the fish to pass through, ensnaring them around the gills when they attempt to escape.

GILL RAKERS Bony, fingerlike projections on the gill arches, located underneath the gill cover or operculum of bony fishes.

HANDLINING Angling with a fishing line held in the hand, without using a rod or reel.

INLET A narrow passage of water connecting the open sea with protected coastal and inland water.

JACK SALMON A term applied to small, but sexually precocious male salmon (chinook or coho) capable of spawning at 2 years of age. Most male chinook and coho mature a year or more later.

JETTY FISHING Fishing from any man-made structure constructed of rock or stone or the like, which projects out into the sea or other body of water.

JIG An artificial lure made to simulate live bait. It is usually made with a lead head cast on a single hook and is heavier than most other lures.

JIGGING Manipulating a jig to imitate a live bait, thus attracting the fish to the hook. The jig can be lowered vertically or cast some distance away, then jerked upward a short distance. Immediately after this upward jerk the lure is allowed to sink back. This procedure is repeated until a fish is hooked, which is usually on the rise of the jig.

LURE An artificial bait.

MOOCHING A method of salmon fishing from a drifting or propelled boat. The bait is sunk deep with a heavy sinker, then brought upward at an angle as the boat is maneuvered forward a few yards or the line retrieved. The bait is then allowed to sink once again to the bottom and the procedure repeated. Usually whole or cut herring is used and rigged so that it has a spinning action in the water.

ORIGIN OF FIN The anterior end of the base of a fin.

PARTY BOAT A fishing boat carrying large groups of anglers for a fee and operating on a scheduled basis. Spaced on the boat is sold to the general public until either the boat is filled to capacity or the scheduled sailing time is reached. The captain usually determines the type of fishing and area to be fished, and the fee usually includes bait but not tackle.

PELAGIC Spoken of fish and other sea animals that are more or less independent of the bottom. They are characteristically active swimmers, spending much of their time in mid-water or near the surface.

PIER FISHING Fishing from any private or public structure set on pilings that extends over a body of water.

PLANKTON A collective term applied chiefly to all those minute and extremely diverse forms of plants and animals that drift with the currents.

PLUG A nonspecific term for any artificial lure having a distinct "body" made of wood or plastic and having one or more sets of single, double, or treble hooks attached. Most plugs are designed to wobble or create a commotion in the water when retrieved.

POKE-POLING A unique method of rocky-shore fishing for blennies and other crevice-seeking animals that

inhabit deep tide pools along the Pacific coast mainland. The gear is essentially homemade. A long bamboo pole of about 9 to 12 feet is fitted with a semiflexible wire tip to which a nylon-cord leader and hook are attached. The bait, usually mussel or shrimp, is "poked" into crevices under and between large boulders in rocky-surge areas at low tide, then retrieved quickly after the first sharp tug of a fish.

POPPER A lightweight artificial lure made of cork or plastic having a concave face that produces a popping sound when twitched on the water's surface. Attracts fish by the commotion it causes in the water.

SCUTE A modified fish scale formed into an external bony or horny plate.

SKIFF FISHING Recreational fishing from a relatively small private or rented boat that does not carry any paying passengers.

SPINNER An artificial lure with metal or plastic blades that whirl on a shaft or a swivel as the lure is retrieved. Attracts fish by the commotion it causes as well as by its flash.

SPINNING A method of rod-and-reel fishing distinguished by the use of a fixed-spool reel or "spinning" reel. When casting, the line slips off the end of the reel spool, which does not revolve as does a conventional bait-casting reel spool. Spinning gear makes it easier to cast very light lures and

avoid backlashes in the line.

SPOON An artificial lure with a curved or dished out body that wobbles but does not revolve. Attracts fish by its movements as well as color.

STILL FISHING Fishing natural baits from shore, pier, or anchored boat. Usually the bait is fished on or near the bottom, although sometimes held off the bottom with a float.

SQUIDDING Casting metal lures called "squids" into the surf. This term is also used in Hawaii to describe fishing for octopus, called "squid" by islanders. When "squidding," one walks out across the reef armed with a spear, looking for octopus with the aid of a glass-bottomed box. Lights are used when fishing at night for "night squid."

SURF FISHING Casting a bait or lure along sandy beaches for fishes that frequent the surf zone. A long flexible rod is usually used to help hurl the bait a maximum distance and to hold the line high enough to clear the breakers. Also called surf casting.

SURF NETTING A unique type of Pacific coast fishing using special one- or two-man nets to catch smelt along sandy beaches. (See also A-FRAME NET.) Generally, there are two separate fisheries—one during the daylight hours for day or surf smelt, and the other at night (and often on the same beaches) for night smelt. The fish are strained from receding breakers as they come into shallow water to

spawn, usually a few hours just before and after high tide.

SURROUND NET A beach seine, typically a long net having floats along the upper edge and weights along the bottom, used to capture an assortment of fishes in shallow protected water. The net is held in place on the shore at one end while the other end is pulled out around the fish to another point farther down the shore line. The net is then pulled slowly to the beach enclosing the fish in a decreasing semicircle. In Hawaii, large-group surround net fishing is called "hukilau."

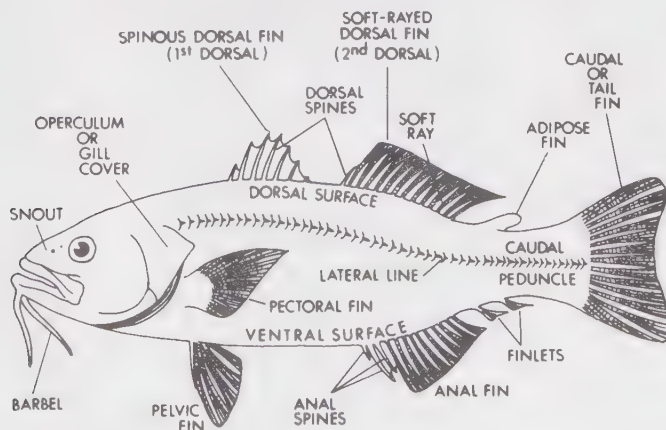
SPEAR FISHING Impaling fish with a spear from either above or below the water's surface.

TORCH FISHING Locating or attracting marine animals at night with a light held above the surface of the water. Torch fishing usually takes place on calm dark nights over shallow reefs at low tide, and when the animal is located, it is either speared or netted.

TROLLING Trailing artificial or natural baits behind a moving boat. The bait can be made to skip along the surface or trailed below at any depth to just above the bottom. A bait or lure trailed behind an angler walking along a pier, bridge, or breakwater is also called trolling.

WATER COLUMN Spoken of the water from the surface to the bottom at a given point.

HYPOTHETICAL FISH SHOWING ANATOMICAL TERMS



Index to Common Names of Fishes

The following is an alphabetical listing of some of the common fish names used by marine anglers who fish along the Pacific coast and around the Pacific Islands. Many times confusion arises when one common fish name such as "snapper" or "bass" refers to more than one species, or when more than one name is used for the same species depending upon the geographical area fished and sometimes even the size of the fish itself. The purpose of this index is to help locate information on the fish described in the Marine Game Fish section. The numbers in this index are not page numbers; they refer to the paragraph numbers preceding each species description on the two fish lists.

A
'a'ala'ihi 214
aaga 213
'a'awa 210
achuman 173
afolu 201
agua 158
aguas 218
'aha'aha 160
'ahi 227
aholehole 167
aji 174
aku 229
akule 174
'alalaua 170
albacore 71
false 228
Allison tuna 72
alu 220
'ama'ama 218
amberjack
for yellowtail 37
greater 172
anchovy, northern 147
asi 227
aso'ama 185
ata'ata 164
Atka mackerel 113
atu 229
atulai 174
atule 174
a'u 232, 234-236
a'u-lepe 233
awa 158
awaawa 156
awa'aua 156

aweoweo 169
B
barberpole
for flag rockfish 107
for treefish 106
barrachen 95
barracuda
California 69
great 220
Japanese 220
Pacific 69
barred surfperch 51
barred sand bass 3
barry 69
bashokajiki 233
bass
barred sand 35
bigeye 150
black
for black croaker 47
for black rockfish 80
black sea 32
blue
for black croaker 47
for opaleye 49
bull 33
calico 33
giant sea 32
ground 35
kelp 33
mountain 167
rock 31
sand 35
spotted sand 34
striped 31
sugar
for barred sand bass 35
for olive rockfish 82
bass rockfish
for black rockfish 80
for olive rockfish 82
bat ray 9
bay perch 55
bigeye bass 150
bigeye, red 169
bigeye rockfish 105
bigeye scad 174
big skate 140
billfish
see marlin, swordfish, sailfish
black bass
for black croaker 47
for black rockfish 80
blackcod 109
black croaker 47
black marlin 234
blackmouth 12
black perch
for black surfperch 55
for opaleye 49
black rockfish 80
black sea bass 32
black skipjack tuna 228

blacksmith 151
for opaleye 49
black snapper 80
blackspot wrasse 210
black surfperch 55
black ulua 180
blanquillo 36
blenny eel 70
blueback
for cutthroat trout 17
for sockeye salmon 15
blueback salmon 15
blue bass
for black croaker 47
for opaleye 49
blue cod
for cabezon 116
for sablefish 109
blue crevally 178
blue-eye perch 49
bluefin tuna 73
bluefish
for blue rockfish 79
bluelined snapper 194
blue marlin 235
blue perch
for blue rockfish 79
for halfmoon 48
blue rockfish 79
blue shark 3
blue spotted grouper 162
blue ulua 178
bocaccio 97
boca dulce 221
bocalao 112
bolina 89
bonefish 157
bonehead 74
bonito, Pacific 74
for aku 229
for kawakawa 228
bonito shark 2
borracho 95
broadbill 76, 232
broadfin flounder 128
brown Irish lord 119
brown rockfish 89
for quillback rockfish 90
brown smoothhound 4
bua 195
buffalo cod 112
buffalo sculpin 120
bull bass 33
bull cod 116
bullfish 116
bullhead
for cabezon 116
for Pacific staghorn sculpin 118
bull trout 19
butterfish
for Pacific pompano 78
for sablefish 109
buttersole 135
button perch 49

C

cabezon 116

calico bass 33

calico rockfish 87

calico surfperch 52

California barracuda 69

California corbina 43

California grunion 30

California halibut 121

California lizardfish 148

California moray 144

California scorpionfish 108

California sheephead 66

California skate 141

California whiting 43

canary rockfish 98

candlefish 22

cardinalfishes 171

Catalina croaker 42

Catalina perch

 for halfmoon 48

 for opaleye 49

Catalina salmon 41

cat shark 6

cefalutano 86

char, Oregon 19

chefra 104

cherna 80

cherne 85

chilipepper 96

China croaker

 for black croaker 47

 for sargo 40

Chinafish 100

China rockfish 86

chinook salmon 12

chub mackerel 75

chub, sea 206

chucklehead 103

chum salmon 16

C-O sole 134

coal cod 109

codalargo 98

cod

 black

 for sablefish 109

 blue

 for cabezon 116

 for sablefish 109

 buffalo 112

 bull 116

 coal 109

 cultus 112

 green 112

 johnny 96

 Pacific 25

 true 25

coho salmon 13

Columbia river trout 17

convictfish

 for flag rockfish 107

 for treefish 106

convict tang 222

copper rockfish 81

corbina, California 43

corsair 101

corvina 43

cowcod 104

cowfish 104

cow rockfish 104

crevalle 177

crevally, bue 178

 jack 177

 thread 175

croaker

 black 47

 Catalina 42

 china

 for black croaker 47

 for sargo 40

 golden 44

 spotfin 44

white 45

yellowfin 42

 for white seabass 41

cultus cod 112

curlfin sole 132

cutthroat trout (sea-run) 17

D

day smelt 20

diamondback 124

diamond turbot 125

dodo 208

dogfish, spiny 139

dog salmon 16

dogtooth tuna 230

Dolly 19

Dolly Varden 19

dolphin 39, 183-184

dolphin, pompano 184

dorado 39

Dover sole 137

dude 101

dusky rockfish 92

E

eagle rays 9

eel

 blenny 70

 California moray 144

 monkeyface 70

 for monkeyface pricklyback 70

 (Pacific Islands) 159

ehu 191

English sole 129

eulachon 22

F

fafaet 198

fall salmon 16

false albacore 228

false mullet 219

fantail 98

fathead 66

feloitega 196

filione 98

filoa 199

flag rockfish 107

flesh-colored rockfish 93

flounders, lefteye 121, 122

flounders, righteye 123-137

flounder, broadfin 128

 fringe 130

 pointed-nose 129

 roundnose 127

 starry 124

 see also sole, turbot, halibut, sanddab

fo 171

fox shark 1

fringed greenling 111

fringe flounder 130

fringehead, onespot 153

funai 194

G

gadao 162, 163, 165, 166

gallo 104

garrupa 83

gatala 163, 165, 166

gatala moana 162

genuine red 95

gialoto 85

giant kelpfish 152

giant sea bass 32

gindai 193

giolo 85

goatfish(es) 201-205

 red 202

 spot 201

golden croaker 44

gopher 86

gopher rockfish 93

 for kelp rockfish 83

grass rockfish 84

gray reef shark 154

gray shark 154

gray smoothhound 5

gray snapper 185

great barracuda 220

greater amberjack 172

greenback 75

green cod 112

greenling, fringed 111

 kelp 110

 painted 115

 red 111

 rock 111

 whitespotted 114

greenling seatrout 110

green parrotfish 215

green snapper

 for filoa 199

 for yellowtail rockfish 85

greenspotted rockfish 103

greenstriped rockfish 102

green sturgeon 11

ground bass 35

grouper(s) 162-166

 blue spotted 162

 salmon 97

grunion, California 30

guili 206

guitarfish(es) 7, 8

H

hagi 182

hahalalu 174

hake, Pacific 27

halalu 174

halfmoon 48

halibut, California 121

 northern 123

 Pacific 123

 southern 121

hammerhead, scalloped 155

Hawaiian salmon 181

hawkfish, spotted 209

herring, Pacific 145

 for queenfish 46

hinalea 213

 for 'a'awa 210

hinalea lauuli 214

hiting 174

hollywood 107

hooligan 22

hornyhead turbot 126

horse mackerel 38

hoshi ulua 178

houndfish 160

humpback parrotfish 217

humpback salmon 14

humpty 66

I

i'a manaia 166

i'a sina 201

ili'ilia segi 225

illioi 178

Irish lord, red 117

 brown 119

ise 160

J

jack(s) 37, 38, 173-182

 spotted 178

 star 178

jack crevally 177

jack mackerel 38

jacksmelt 28

Japanese barracuda 220

johnnies 96

johnny cod 96

juarel 37

K
 kagami ulua 175
 kahala 172
 kakaka 196
 kaku 220
 kala 225
 kalikali 189
 pink 189
 yellowtail 187
 kamanu 181
 kawalea 220
 kawakawa 228
 keeltail needlefish 160
 kelp bass 33
 kelpfish, giant 152
 for kelp greenling 110
 kelp greenling 110
 kelp rockfish 83
 for grass rockfish 84
 kelp salmon 82
 kelp surfperch 62
 kelp yellowtail 82
 kicho 222
 kiluus 155
 king 12
 kingfish 45
 king salmon 12
 kumu 204
 kupipi 208
 kurokajiki 235

L
 ladyfish 156
 lae 182
 lai 182
 lansi 171
 leatherback 182
 leatherjacket 182
 lehi 192
 lemon sole 129
 leopard shark 6
 liguan 218
 lililok 199
 ling 112
 lingcod 112
 little mahimahi 184
 little tunny 228
 lizardfish, California 148
 loalia 200
 longfin smelt 23
 longfin sole 131
 longfin tuna 71
 longnose skate 142
 lupo, see jacks, 177-180

M
 ma'au 174
 mackerel
 Atka 113
 chub 75
 horse 38
 jack 38
 Pacific 75
 Spanish
 for jack mackerel 38
 striped 75
 for akule 174
 for sablefish 109
 mackerel scad 173
 mahimahi 39, 183
 little 184
 makajiki 236
 mako, shortfin 2
 mala'i 198
 malau 161
 malaui 175
 malie 154
 malma trout 19
 malu 203
 mamagas 169
 mamamu 200
 mamu 207

manaloa 206
 manini 222
 mano 154
 mano kihikihi 155
 maomao 207
 marbled sculpin 116
 marlin
 black 234
 blue 235
 striped 77, 236
 masimasi 183
 mata-i-taliga 155
 matanhagon 200
 mata-pula 169
 mekajiki 232
 mempachi ulua 179
 menpachi 161
 midshipman
 northern 149
 plainfin 149
 milkfish 158
 moano 205
 moi 221
 moi-li'i 221
 monkeyface eel 70
 monkeyface prickleback 70
 moonlight Annie 171
 moonlight fish 171
 moray
 California 144
 (Pacific Islands) 159
 mottled sanddab 122
 mountain bass 167
 mu
 for *Lutjanus bohar* 197
 for *Monotaxis grandoculus* 200
 mullet 218
 false 219
 striped 218
 mumu moaga 200

N
 naraigi 236
 needlefish(es) 160
 keeltail 160
 nenue 206
 nenue parii 206
 nero 80
 night smelt 21
 nohu 237
 nohu omakaha 237
 northern anchovy 147
 northern halibut 123
 northern midshipman 149

O
 oama 201
 ocean whitefish 36
 'o'io 157
 oliveback rockfish 105
 olive rockfish 82
 'omaka 176
 'omilu 178
 'omilumilu 178
 onaga 190
 onespot fringehead 153
 ono 231
 'o'opu-kai 209
 'opakapaka 186
 yelloweye 188
 opaleye 49
 'opelu 173
 'opelu-mama 173
 orange rockfish 98
 orange-spotted rockfish 90
 Oregon char 19
 oshi 178

P
 Pacific barracuda 69
 Pacific bonito 74
 Pacific cod 25

Pacific hake 27
 Pacific halibut 123
 Pacific herring 145
 Pacific mackerel 75
 Pacific pompano 78
 Pacific sanddab 122
 Pacific sardine 146
 Pacific staghorn sculpin 118
 Pacific sturgeon 10
 Pacific threadfin 221
 Pacific tomcod 26
 painted greenling 115
 paka, pink 186
 pake 'awa 156
 pake ulua 179
 palani 224
 palu 190
 papio, see jacks, 177-180
 parrotfish, green 215
 humpback 217
 pa'u'u 177
 perch
 bay 55
 black
 for black surfperch 55
 for opaleye 49
 blue
 for blue rockfish 79
 for halfmoon 48
 blue-eye 49
 button 49
 Catalina
 for halfmoon 48
 for opaleye 49
 silver
 for aholehole 167
 for silver surfperch 54
 see also surfperch(es)
 petrale sole 127
 pile surfperch 58
 pink kalikali 189
 pink paka 186
 pink salmon 14
 pink snapper 186
 pink surfperch 65
 plainfin midshipman 149
 pointed-nose flounder 129
 pompano dolfin 184
 pompano, Pacific 78
 po'o-pa'a 209
 po'ou 211
 popeye rockfish 105
 porgy 50
 potbelly 99
 prickleback, monkeyface 70
 priestfish 79
 pualu 223
 puhi 159
 puhi-paka 159
 pulus 160
 pusi 159

Q
 queenfish 46
 quillback rockfish 90
 Quinnot salmon 12

R
 rabbitfish 226
 rainbow runner 181
 rainbow surfperch 60
 rainbow trout (sea-run) 18
 rasher 95
 rasphead rockfish 99
 ray, bat 9
 redband rockfish 107
 red bigeye 169
 redfish 66
 red goatfish
 for kumu 204
 for weke-'ula 202

red greenling 111
 red Irish lord 117
 red-margined sea perch 195
 red rock cod (see rockfishes, red)
 red salmon 15
 red snapper
 for mala'i 198
 for onaga 190
 for vermilion rockfish 95
 for yelloweye rockfish 99
 for canary rockfish 98
 redtail surfperch 50
 red-spotted trout 19
 red weke 202
 reina 102
 rex sole 131
 rock bass
 for striped bass 31
 rock cod (see rockfishes)
 rockfish(es) 79-106
 barberpole 107
 for treefish 106
 bass
 for olive rockfish 82
 for black rockfish 80
 bigeye 105
 black 80
 blue 79
 bocaccio 97
 brown 89
 for quillback rockfish 90
 calico 87
 canary 98
 chilipepper 96
 china 86
 copper 81
 cow 104
 dusky 92
 flag 107
 flesh-colored 93
 gopher 93
 for kelp rockfish 83
 grass 84
 greenspotted 103
 greenstriped 102
 hollywood 107
 kelp 83
 for grass rockfish 84
 olive 82
 oliveback 105
 orange 98
 orange-spotted 90
 popeye 105
 quillback 90
 rasphead 99
 red
 for canary rockfish 98
 for vermilion rockfish 95
 for yelloweye rockfish 99
 redbanded 107
 rosy 101
 silvergray 91
 smallmouth 94
 Spanish flag 107
 speckled 90
 spotted 100
 squarespot 94
 starry 100
 stripetail 105
 turkey-red 99
 vermilion 95
 widow 88
 whitebelly 81
 yellow-backed 90
 yelloweye 99
 yellowtail 85
 rock greenling 111
 rock sole 128
 rock trout 110
 rock wrasse 67
 roi 162
 roncky 45

roosterfish
 for cow rockfish 104
 rosy rockfish 101
 roundnose flounder 127
 round stingray 143
 rubberlip surfperch 57
 rudderfish 206
 runner, rainbow 181
 for lae 182

 S
 sablefish 109
 saddle wrasse 214
 sailfish 233
 salema 150
 salmon, blackmouth 12
 blueback 15
 Catalina 41
 chinook 12
 chum 16
 coho 13
 dog 16
 fall 16
 Hawaiian 181
 humpback 14
 king 12
 pink 14
 Quinnat 12
 red 15
 silver 13
 sockeye 15
 spring 12
 tyee 12
 white 37
 salmonete 201
 salmonete acho 203
 salmonete manining 202
 salmon grouper 97
 salmon trout
 for coho salmon 13
 for Dolly Varden 19
 for steelhead (rainbow trout) 18
 sand bass 35
 spotted 34
 barred 35
 sanddab
 mottled 122
 Pacific 122
 sand shark 154
 sand sole 130
 Santa Maria 103
 sapatu 220
 sardine, Pacific 146
 sargo 40
 sasag 161
 sasele 168
 saula 235
 saula-lele 233
 saurel 38
 savani 194
 scacciatale 101
 scad
 bigeye 174
 mackerel 173
 scaleless tuna 230
 scalloped hammerhead 155
 scomoda 84
 scooter 69
 scorpionfish 237
 California 108
 scratch-tail 101
 sculpin
 buffalo 120
 marbled 116
 Pacific staghorn 118
 smooth 118
 for California scorpionfish 108
 seabass
 white 41
 see also bass
 sea chub 48-49, 206

sea perch
 red margined 195
 yellow-and-blue 194
 see also surfperch(es)
 sea-run cutthroat trout 17
 sea-run rainbow trout 18
 seatrout
 for cutthroat trout 17
 for Dolly Varden 19
 for greenling 110
 for steelhead 18
 for white seabass 41
 señorita 68
 serena 102
 sergeant major 208
 sesjun 226
 shark
 blue 3
 bonito 2
 brown smoothhound 4
 cat 6, 138
 fox 1
 gray 154
 gray reef 154
 gray smoothhound 5
 leopard 6
 sand 154
 scalloped hammerhead 155
 shortfin mako 2
 shovelnose 7
 swell 138
 swiveltail 1
 thresher 1
 whaler 154
 sharpnose surfperch 64
 sheephead, California 66
 shiner surfperch 61
 shiner, yellow 61
 shirokajiki 234
 shofflies 107
 shortfin mako 2
 shovelnose guitarfish 7
 shovelnose shark 7
 silvergray rockfish 91
 silver perch
 for aholehole 167
 for silver surfperch 54
 silver salmon 13
 silversides
 for coho salmon 13
 for rainbow trout (steelhead) 18
 see also smelt(s)
 silver smelt 20
 silver surfperch 54
 skate
 big 140
 California 141
 longnose 142
 skil 109
 skipjack tuna 229
 black 228
 slender sole 136
 smallmouth rockfish 94
 smelt(s) 20-24
 day 20
 longfin 23
 night 21
 silver 20
 surf 20
 whitebait 24
 for eulachon 22
 for jacksmelt 28
 for topsmelt 29
 smooth sculpin 118
 snapper(s) 185-198
 black
 for black rockfish 80
 blue-lined 194
 gray 185
 green
 for filoa 199
 for yellowtail rockfish 85

pink 186
 red
 for canary rockfish 98
 for mala'i 198
 for onaga 190
 for vermilion rockfish 95
 for yelloweye rockfish 99
 yellow
 for canary rockfish 98
 see also rockfish(es)
 sockeye salmon 15
 sole
 butter 135
 C-O 134
 curlfin 132
 Dover 137
 English 129
 lemon 129
 longfin 131
 petrale 127
 rex 131
 rock 128
 sand 130
 slender 136
 southern halibut 121
 Spanish flag 107
 Spanish mackerel
 for jack mackerel 38
 speckled rockfish 90
 spiny dogfish 139
 spotfin croaker 44
 spotfin surfperch 63
 spot goatfish 201
 spotted hawkfish 209
 spotted jack 178
 spotted rockfish 100
 spotted sand bass 34
 spotted turbot 133
 spot weke 201
 spot wrasse 210
 spring salmon 12
 squarespot rockfish 94
 squirrelfish(es) 161
 staghorn sculpin, Pacific 118
 star jack 178
 starry flounder 124
 starry rockfish 100
 steelhead 18
 stingray, round 143
 strawberry rock cod 102
 striped bass 31
 striped mackerel 75
 striped marlin 77, 236
 striped mullet 218
 striped surfperch 56
 striper 31
 stripetail rockfish 105
 sturgeon
 green 11
 Pacific 10
 white 10
 sugar bass
 for barred sand bass 35
 for olive rockfish 82
 surffish
 for California corbina 43
 for smelt 20, 21
 surfperch
 barred 51
 black 55
 calico 52
 kelp 62
 pile 58
 pink 65
 rainbow 60
 redtail 50
 rubberlip 57
 sharpnose 64
 shiner 61
 silver 54

spotfin 63
 striped 56
 walleye 53
 white 59
 surf smelt 20
 surgeonfish(es) 222-225
 swell shark 138
 swiveltail 1
 swordfish 76, 232

T
 ta'ape 194
 tagi 230
 tagafi 197
 taiva uli'uli 196
 tambor 99
 tang, convict 222
 tangisun 212
 tanifa 154
 tarakitiyos 177, 178-180
 see jacks
 tarakito 177, 178-180
 see jacks
 tataga 225
 teau 201
 ten-pounder 156
 thornback 8
 thread crevally 175
 threadfin, Pacific 221
 thresher shark 1
 tiger 107
 titugi 159
 toau 195
 tomcod
 Pacific 26
 for young bocaccio 97
 for white croaker 45
 topmelt 29
 iosun 231
 treefish 106
 trout
 blueback 17
 bull 19
 Columbia River 17
 cutthroat (sea-run) 17
 Dolly Varden 19
 malma 19
 rainbow (sea-run) 18
 red-spotted 19
 rock 110
 salmon
 for coho salmon 13
 for Dolly Varden 19
 for steelhead (rainbow trout) 18
 steelhead 18
 true cod 25
 tuna
 albacore 71
 Allison 72
 black skipjack 228
 bluefin 73
 dogtooth 230
 longfin 78
 scaleless 230
 skipjack 229
 white 230
 yellowfin 72, 227
 tunny, little 228
 turbot
 diamond 125
 hornyhead 126
 spotted 133
 turkey-red rockfish 99
 turkey rock 99
 tyee 12
 U
 ugupao
 for palani 224
 for pualu 223

uhu
 for *Scarus perspicillatus* 215
 for *Scarus dubius* 216
 uku 185
 ula oa 202
 'ula'ula 191
 'ula'ula koae 190
 ulua
 black 180
 blue 178
 hoshi 178
 kagami 175
 mempachi 179
 pake 179
 white 175
 ulua kihikihi 175
 umatan 168
 ume 225
 unicornfish 225
 uouoa 219
 'upapalu 171
 'u'u 161

V
 vava sui 196
 vermilion rockfish 95
 vete 202
 viuva 88

W
 wahoo 231
 walleye surfperch 53
 weke
 red 202
 spot 201
 weke-'a'a 201
 weke-'ula 202
 whaler 154
 whitebait smelt 24
 whitebelly rockfish 81
 white croaker 45
 whitefish, ocean 36
 white salmon 37
 white seabass 41
 whitespotted greenling 114
 whitesurfperch 59
 white sturgeon 10
 white tuna 230
 white ulua 175
 whiting
 for ocean whitefish 36
 for California corbina 43
 widow rockfish 88
 wrasse(s) 66-68, 210-214
 blackspot 210
 rock 67
 saddle 214
 spot 210

Y
 yellow-and-blue seaperch 194
 yellow-backed rockfish 90
 yelloweye opakapaka 188
 yelloweye rockfish 99
 yellowfin croaker 42
 yellowfin tuna 72, 227
 yellow shiner 61
 yellow snapper
 for canary rockfish 98
 yellowtail 37
 kelp 85
 for yellowtail rockfish 85
 yellowtail rockfish 85
 yellowtail kalikali 187

Z
 zebra 75

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USE OF AIRBORNE RADIOMETERS FOR MONITORING SEA SURFACE TEMPERATURE AND CHLOROPHYLL IN A COASTAL FISHING ZONE

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ABSTRACT

The need for monitoring the rapidly changing coastal marine environment and using this information in the assessment of a coastal fishery such as the California anchovy is noted. Previous measurements of sea surface temperature and relative chlorophyll concentration suggest that these are two important biological parameters that can be rapidly obtained in a synoptic fashion from a suitably equipped aircraft. Experimental flights with a twin engine Beechcraft Travel Air aircraft equipped with a modified precision radiation thermometer (PRT-5) infrared radiometer and a dual channel differential radiometer (DCDR) for ocean color were made on several occasions in late 1974, and the results from the 4 and 9 October flights are briefly described. Analysis of these flight data suggest that by careful evaluation of the strip chart records, statistically significant relationships can be obtained between both remote sensors. While quantitative results depend upon reasonably frequent ground-truth observations for both radiometers, particularly the DCDR instrument, a rough conversion to $\text{mg chlorophyll}/\text{m}^3$ for the DCDR was made based on limited surface chlorophyll *a* measurements and published calibration curves. The results suggest that when the design constraints of the DCDR instrument are recognized and the instrument is used in conjunction with the PRT-5 radiometer the paired radiometers offer considerable potential for monitoring two biologically important parameters in a coastal fishing zone.

RESUMEN

Se indica que es necesario supervisar los cambios rápidos que se presentan en el ambiente marino costero y usar esta información en la pesca superficial, como es la pesca de la anchoveta californiana. Las medidas tomadas anteriormente de la temperatura superficial del mar y, de la concentración relativa de clorofila indican que estos son dos parámetros biológicos importantes que pueden obtenerse rápidamente de una manera sinóptica desde un avión equipado convenientemente. A fines de 1974 se realizaron en varias ocasiones vuelos experi-

mentales con un bimotor Beechcraft Travel Air, equipado con un radiómetro modificado infrarojo PRT-5 y un radiómetro diferencial de doble banda (Dual Channel Differential Radiometer [DCDR]) para obtener datos sobre el color del océano, y se describen brevemente los resultados de los vuelos realizados entre el 4 y 9 de Octubre. El análisis de los datos de estos vuelos indican que al evaluar cuidadosamente los registros del aparato de banda, se pueden obtener relaciones estadísticamente significativas entre los dos sensores remotos. Aunque los resultados cuantitativos dependen de las observaciones terrestres reales, obtenidas con frecuencia razonable de ambos radiómetros, especialmente del instrumento (DCDR), con respecto a este instrumento se hizo una conversión preliminar a $\text{mg de la clorofila}/\text{m}^3$ basadas en medidas limitadas de la clorofila *a* en la superficie y de publicaciones de las curvas de calibración. Los resultados indican que cuando se reconocen las limitaciones del trazado del instrumento DCDR y se usa éste junto con el radiómetro PRT-5, los dos radiómetros ofrecen un potencial considerable para la supervisión de los dos parámetros biológicamente importantes en una zona costera de pesca.

INTRODUCTION

Both coastal fisheries and pelagic fisheries respond to changes in the environment, but coastal conditions may frequently undergo greater changes than conditions in the open ocean. The famous anchovy (*Engraulis ringens*) fishery off Peru is located in a coastal upwelling regime where horizontal surface temperature gradients of $3^\circ\text{C}/50 \text{ km}$ may occur and give rise to fluctuations in the phytoplankton populations and corresponding surface chlorophyll gradients of $3 \text{ mg}/\text{m}^3$ (Beers et al. 1971). Higher trophic levels such as the anchovy are in turn dependent upon the standing crop of the phytoplankton. An adequate understanding of the presence and variability of a regional coastal fishery, then, depends upon the scientists' ability to monitor the rapidly changing environment and to determine how coastal fish stocks respond to these changes in the environment.

Two of the more important parameters used to monitor the marine environment are surface temperature (may indicate relative intensity and duration of upwelling) and chlorophyll (estimates standing crop of phytoplankton). In principle it would be desirable to make weekly, if not daily, ship surveys of the coastal zone to monitor these and other important parameters. In most instances, however, ship time is expensive and, therefore, limits such surveys to several-day cruises. A method that can rapidly scan a long coastal zone and provide environmental data of reasonable accuracy would represent an optimum method of obtaining the needed environmental information in order to make indirect assessment of some fish stocks of the coastal waters. Stevenson and Miller (1974) have correlated tuna fish catch with sea surface temperature in a region 1800 km west of California, although cloud cover was a problem. Intervening clouds may be more of a problem in coastal zones, and in those regions a low-flying aircraft using remote sensors may be ideally suited for the job.

Airborne survey flights to assess apparent fish abundance have been made commercially for a number of years. Squire reports (1972) that it is feasible to estimate fish school tonnage from commercial spotter aircraft flights over the coastal zone of California from the Los Angeles Bight south to the Mexican border. Squire's study is based on more than 17,000 flight hours made during 1962-69. More recently Squire has made survey flights to monitor sea surface temperature patterns for correlation with change in catch and catch rates for several coastal species. Sea surface temperatures were determined with a Barnes' PRT-5 radiometer from an aircraft. Arvesen et al. (1973) have developed an extremely compact instrument for detecting changes in ocean color, the dual channel differential radiometer (DCDR). He has flown the DCDR and PRT-5 radiometer off the California coast where, during an offshore transect, he obtained an inverse pattern between sea surface temperature and chlorophyll concentration.

During September-October 1974, a visit was made by Professor Ikeda to the Inter-American Tropical Tuna Commission (IATTC) headquarters, at the National Marine Fisheries Service (NMFS) Laboratory in La Jolla, to investigate methods of using airborne and spacecraft data in the field of fishery oceanography. After some discussions by the first two authors with Ikeda, several instructional/experimental flights using the NMFS PRT-5 radiometer were made off the southern coast of California. It then came to our attention that Dr. Arvesen's DCDR ocean color radiometer was on loan to Mr. Booth of the Institute of Marine Resources (IMR), and we invited Mr. Booth to participate in joint flights where both the DCDR and PRT-5 instruments might be flown together.

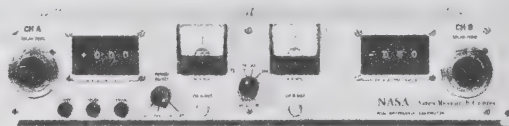


Figure 1. (Upper) Modified precision radiation thermometer (PRT-5) mounted in aircraft. Scientific observer sits in opposite seat to make time and position annotations on charts produced by the PRT-5, and the (lower) dual channel differential radiometer (DCDR).

INSTRUMENTS AND METHODS

Two radiometers were used from the aircraft normally chartered by NMFS for its sea surface temperature survey flights, etc. (Figure 1). The NMFS instrument, a modified PRT-5 radiometer equipped with a 10.5-12.5 micron filter, together with a strip chart recorder and power supply, were mounted to a miniature instrument rack. The rack was attached to the positioning frame of a passenger seat in the rear of the plane after the seat had been removed from the aircraft. The access port for instruments was located directly behind the rear cabin bulkhead and was reached by

removal of the bulkhead prior to the flights.

The DCDR instrument was developed by Dr. John Arvesen of the NASA/AMES Center and was available through his courtesy for field experiments. Because a detailed description of the system's specifications is found in Arvesen et al (1973), only a brief explanation is given here. The DCDR is a rack-mounted, all solid-state instrument and requires a conventional strip chart recorder for output. The color sensor consists of a wide-angle field of view lens cemented to one end of a fiber optics cable. The fiber optics bundle is split at the other end into four smaller bundles. Each of these is arranged so that the emerging light passes through a narrow band interference filter and strikes a silicon diode detector. The chlorophyll sensing is accomplished by use of two of these detector-filter combinations. One combination uses a 525- μm band-pass filter for the reference signal as this is the wavelength region of minimum attenuation due to chlorophyll. The other detector-filter combination has a 443- μm band-pass filter which is an absorption maximum for chlorophyll *a*. The ratio of the light from the fiber optic bundle striking these detector-filter combinations is calculated by the instrument and displayed on a strip chart recorder. During an experiment the probe is pointed downward at an angle (approximately 15°) to minimize the reflected glitter on the ocean surface. The probe is occasionally pointed at or toward an unobstructed view of the sun during each flight, and the DCDR instrument's gain is normalized at that time. For the experiments described in this paper, the PRT-5 instrument rack was modified to accommodate the DCDR instrument and a Hewlett Packard Mosley strip chart recorder. The power for both PRT-5 and DCDR instruments was obtained from the aircraft's electrical generators. For simultaneous operation of the two radiometers, a cylindrical flange was made and attached to the circumference of the access port so that the narrow beam PRT-5 sensor head was axially aligned through the port. Special slots were cut into the flange to accommodate the DCDR probe. While the two probes were not exactly coaxially aligned, the wide-angle field of view of the DCDR probe assured adequate overlap of the viewing targets of the two radiometers.

The principal problem with the DCDR is its dependence on constant solar illumination of the sea surface. This problem has two parts. First, atmospheric conditions must be uniform over the flight path so that the spectral composition and intensity of the light incident on the sea surface remains constant. This drawback may be compensated for by repetitive standardization by viewing the sun with the probe. This limits flights to days with uniform clearness. The second problem arises when the airplane changes headings, thus changing the probe viewing angle relative to the angle of the sun and resulting change in the amount of back reflection or "glit-

ter" from the sea surface. Efforts to compensate for this effect by changing the position of the probe are never wholly satisfactory. This effect tends to bias the signal to the null position, which corresponds to 1 mg/m³ chlorophyll *a*. It is very difficult to correct for this effect on the present instrument, although we hope to make certain modifications in the future to reduce the instrument's sensitivity to glitter.

Calibration for the PRT-5 was provided by flying over the Naval Electronics Laboratory (NEL) tower located about 3 km offshore from San Diego. In previous flights with the NMFS PRT-5 instrument, Squire found the corrected airborne temperature data to be within 0.1-0.2°C of temperatures measured from the NEL tower. The calibration of the DCDR instrument was accomplished in a similar fashion. The DCDR does not provide readout directly in units of chlorophyll but rather in volts. To convert the volts into mg chlorophyll *a*/m³, one or more surface water samples are collected beneath the flight path and chemically analyzed for chlorophyll *a* concentration, and the DCDR data are then converted from volts into chlorophyll units.

FIELD EXPERIMENTS

Because the time available to make the cooperative flights fell within the time frame of the NMFS sea-surface temperature survey flights, we decided to use the NMFS flight track to make simultaneous measurements with both radiometers. One observer sat in the starboard rear seat in order to operate the radiometer recorders mounted on the port side; a second observer sat in the copilot's seat and assisted with general flight operations. Flights using both PRT-5 and DCDR instruments were made on 4 and 9 October 1974. The same general flight plan was followed each time. Since the flight observations were also similar, only the October 4 flight will be discussed. The aircraft flew from a local San Diego airport over the coastal water at 150 m altitude starting at 1150 PDT, and the flight track was terminated at 1330 PDT after which the aircraft returned to the same airfield. During the flight the aircraft flew over the NEL tower twice to obtain sea surface calibration temperatures for the PRT-5 data. The DCDR uses a solar reference, and during cloud-free conditions, when properly normalized, provides a reasonably stable output signal. During the flight a calibration of the DCDR was conducted by twice passing over a boat where surface water sample was collected for chlorophyll *a* analysis. The boat was located about 1.5 km off the Scripps pier.

RESULTS

After the 3.5-hour flight, the strip chart records were checked for proper time and position annotations, and the charts were then manually digitized. PRT-5 data

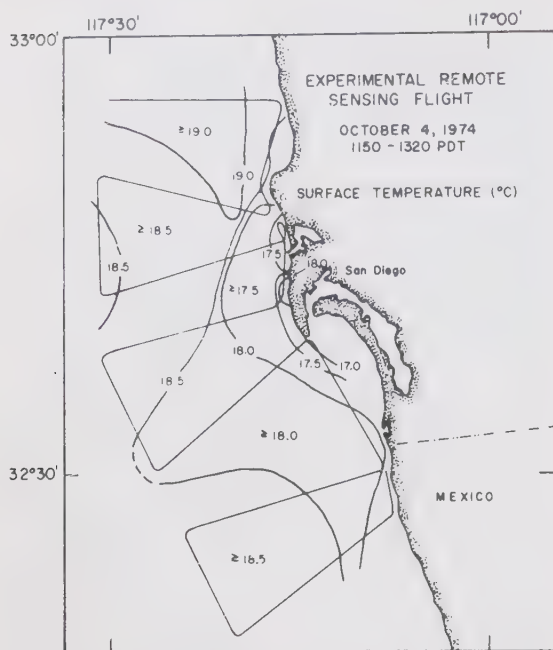


Figure 2. Sea surface temperature map for 4 October 1974, based on Barnes PRT-5 radiometer data. Blackbody thermal radiation is measured continuously as the aircraft moves along its flight path.

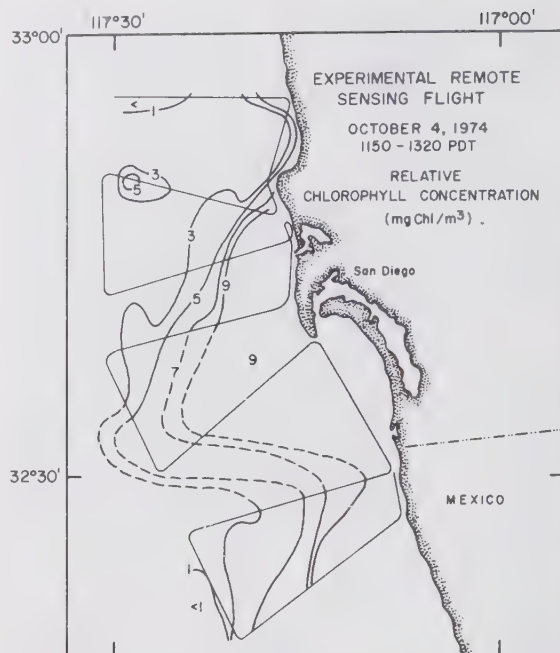


Figure 3. Relative chlorophyll concentration map for 4 October 1974, based on the DCDR ocean color instrument data. The intensity measurements of 443 μm ocean color, which change in response to chlorophyll concentration are referenced to 525 μm radiation, which undergoes minimal change due to the presence of chlorophyll.

were calibrated with the NEL tower temperature data, and the calibrated temperatures were used to construct a contoured map of the surface temperature shown in Figure 2. Ocean color data from the DCDR instrument was similarly digitized and calibrated with the surface chlorophyll measurements off Scripps Pier, and the data were used to construct the surface chlorophyll map shown in Figure 3.

For statistical purposes, the analog records were read at 1-minute intervals to form data pairs. A comparison of the PRT-5-derived surface temperatures and DCDR-derived Chlorophyll Index data (CI) obtains a correlation coefficient for the 4 and 9 October experiment of $r = -0.49$ and -0.60 ($P = 1\%$ level), respectively, and the following relationships:

$$\begin{aligned} \text{CI} &= -0.58T + 21 \text{ and} \\ \text{CI} &= -0.55T + 12.8 \end{aligned}$$

respectively, where the slopes are the conversion constants from Chlorophyll Index (volts) to surface water temperature. Analysis of the individual strip charts shows considerable "small structure," appreciable gradients in temperature that extend over distances of several hundreds of meters. Because one surface measurement of chlorophyll was made on 4 October, it was only possible to roughly calibrate the DCDR data. The result of the

calibration is based on data from Arvesen et al. (1973) and for $0 < \text{CI} < 3$ volts is

$$\text{chl } a = 0.58(\text{CI} - 7.6)^2 + 1.2,$$

where 0.58 is the conversion rate from volts to 1.2-6.5 mg chl a/m^3 and 7.6 and 1.2 are voltage and recorder curve offsets. For lower concentration levels, i.e. $0.1 < \text{chl } a < 1 \text{ mg}/\text{m}^3$, an approximate conversion is

$$\text{chl } a = 0.027 (\text{CI} - 1.4)^2 + 0.092.$$

It should be recognized that the conversion from Chlorophyll Index to chl a is only approximate unless the conversion can include the effects of non-chlorophyll suspended sediment and more calibration points.

Due to a lack of fish school sightings during the flights, it was not possible to compare locations of fish schools with thermal and chlorophyll fronts. Squire, however, has noted (manuscript 1975) that when albacore concentrations are present and observed off central California, they are often found on the seaward (warm) side of thermal fronts. Other studies, e.g. Stevenson and Miller (1974), have shown that tropical and subtropical tunas are frequently found along edges of pronounced

thermal gradients or fronts. Because anchovy, at least in their early life, feed first upon phytoplankton and later upon zooplankton which in turn feed upon phytoplankton, it is important to make comparisons of apparent abundance of anchovy schools relative to concentrations of chlorophyll (phytoplankton). Aircraft surveys similar to those described in this paper may determine whether or not distribution of anchovy larvae and adult schools off southern California and Baja California is related to measurements made with infrared radiometry and airborne ocean color radiometer without the measurements of the intermediate zooplankton trophic level. Thus far no researchers have shown the feasibility of directly monitoring zooplankton by remote sensor. The question to be answered is whether or not information on zooplankton abundance must also be available or whether sufficient information about the presence of the anchovy can be obtained from aerial infrared and multispectral radiometry. Future airborne survey flights are needed to address this question.

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EARLY DEVELOPMENT OF SEVEN FLATFISHES OF THE EASTERN NORTH PACIFIC WITH HEAVILY PIGMENTED LARVAE (PISCES, PLEURONECTIFORMES)

B. Y. SUMIDA, E. H. AHLSTROM, AND H. G. MOSER¹

ABSTRACT

Eggs and larval series are described for six species of flatfishes occurring off California with heavily pigmented larvae. These are the pleuronectids *Pleuronichthys coenosus*, *P. decurrens*, *P. ritteri*, *P. verticalis*, and *Hypsopsetta guttulata* and the bothid, *Hippoglossina stomata*. A brief description of postflexion larvae of the Gulf of California species, *P. ocellatus*, is also presented.

Eggs of *Pleuronichthys* are unusual among flatfishes in possessing a sculptured chorion composed of a network of polygonal walls, whereas the chorions of *Hypsopsetta guttulata* and *Hippoglossina stomata* eggs are smooth and unornamented. Eggs of *Hypsopsetta guttulata* and *P. ritteri* are unusual among those of pleuronectid flatfishes in possessing an oil globule.

A combination of pigmentation, morphology, and meristics can distinguish the seven species of flatfishes with heavily pigmented larvae. Larvae of two species, *H. guttulata* and *P. decurrens*, have a distinctive pterotic spine on either side of the head. Sizes at hatching, at fin formation, and at transformation are important considerations to distinguish these species. Meristic counts, particularly of precaudal and caudal groups of vertebrae, are important to relate a larval series to its juvenile and adult stages and thus substantiate identification of the series.

This report deals primarily with the eggs, larvae, and early juveniles of flatfishes of the genus *Pleuronichthys*. Descriptions are included for complete series of larvae of four species, *P. decurrens* (curlfin turbot),² *P. coenosus* (C-O turbot), *P. verticalis* (hornyhead turbot), and *P. ritteri* (spotted turbot). A brief account of postflexion larvae of the Gulf of California species, *P. ocellatus* (Gulf turbot), is also given. Larvae of *Pleuronichthys* are heavily pigmented, even at hatching, as are those of the pleuronectid, *Hypsopsetta guttulata* (diamond turbot), and the bothid, *Hippoglossina stomata* (bigmouth sole). To identify heavily pigmented flatfish larvae obtained in plankton collections from the eastern North Pacific, it is necessary to know the larval developmental series of all of the above species. These species comprise minor incidental catches within California commercial and sport fisheries and are reported as a general

grouping of "turbot." Species most commonly caught in the fisheries are *P. decurrens*, *P. coenosus*, *P. verticalis*, and *Hypsopsetta guttulata* (Frey 1971; Bell 1971; Oliphant 1973; Pinkas 1974; McAllister 1975). No specific catch data are available for *Hippoglossina stomata*, but the species is probably caught incidentally and included in the "miscellaneous sole" category of catch data.

In a review of the genus *Pleuronichthys*, Fitch (1963) recognized six species including the five listed above and *P. cornutus* from off Japan and China. In an earlier review of the genus, Starks and Thompson (1910) recognized these six species and *P. nephelus* Starks and Thompson. Norman (1934) concurred with Starks and Thompson in recognizing seven species. Fitch (1963), however, agreed with Hubbs (1928) in finding no grounds for the separation of *P. nephelus* from *P. coenosus* after his examination of the type material of *P. nephelus*. Fitch's review is thorough; he examined more than 5,700 individuals of the genus. We follow his classification.

The first descriptions of the eggs and early-stage larvae of *Pleuronichthys* were given by Budd (1940) who dealt with *P. coenosus*, *P. decurrens*, and *P. verticalis*. Orton and Limbaugh (1953) described the eggs of *Hypsopsetta guttulata* and *P.*

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²The common name turbot is used for all species of *Pleuronichthys*, a usage consistent with Fitch (1963), Miller and Lea (1972), and Gates and Frey (1974:79). The American Fisheries Society's list of common names (Bailey et al. 1970) designates *P. coenosus* and *P. decurrens* as soles, but we disagree with giving species within a genus different common general names.

ritteri. Larvae of *P. verticalis* were illustrated in Ahlstrom and Moser (1975), and Eldridge (1975) described and illustrated larvae of *H. guttulata*.

MATERIALS AND METHODS

Eggs, larvae, and some juveniles were primarily obtained from California Cooperative Oceanic Fisheries Investigations (CalCOFI) collections. These samples were preserved in a consistent manner as described in Kramer et al. (1972). Additional material was obtained from bay, estuarine, and coastal collections of Occidental College; Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service; California State University at Fullerton; Scripps Institution of Oceanography; Oregon State University; and Humboldt State University. Specimens of *P. ritteri*, *P. verticalis*, and *H. guttulata* reared at the Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, were also utilized.

Egg and oil globule diameters were measured using an ocular micrometer in a stereomicroscope. For eggs that were not perfectly round, the greatest diameter was recorded. Scanning electronmicrographs were made for four kinds of *Pleuronichthys* eggs and for eggs of *Synodus lucioceps* (Synodontidae). The greatest diameter of 10 randomly selected polygonal facets of the chorion of *Pleuronichthys* and *Synodus* eggs were measured using an ocular micrometer in a compound microscope. To do this the chorion was cut into pieces that were laid flat on a glass slide with a cover slip over them.

The number of specimens examined varied by species, depending on their availability and abundance, ranging from several hundred larvae of *P. verticalis*, the most abundant species, to two larvae of *P. ocellatus*. For most species, the minimum number of specimens studied is indicated in the morphometric tables with usually twice as much material looked at for pigmentation development. A developmental series of larvae through juveniles was assembled for each species. Measurements of selected body parts were taken to provide descriptive and comparative morphometric data. Measurements were made on the right side of each pleuronectid specimen, and on the left side of the bothid, *Hippoglossina stomata*, using an ocular micrometer in a stereomicroscope. Terminology used in the morphometric tables is as follows:

Body length = In preflexion and flexion stages, horizontal distance from tip of snout to tip of notochord, referred to as notochord length (NL); in postflexion stages, from tip of snout to posterior margin of hypural elements, i.e., standard length (SL).

Snout to anus = Horizontal distance from tip of snout through midline of body to vertical through anus.

Head length = Horizontal distance from tip of snout through midline of head to margin of cleithrum preceding the pectoral fin base.

Snout length = Horizontal distance from tip of snout to anterior margin of pigmented region of eye.

Eye width = Horizontal distance through midline of pigmented eye.

Eye height = Vertical distance through center of pigmented eye.

Body depth at pectoral base = Vertical distance across body at pectoral fin base prior to formation of dorsal fin pterygiophores. An asterisk follows this measurement in the morphometric tables when it includes the depth of dorsal fin pterygiophores.

Body depth at anus = Vertical distance across body at anus prior to formation of dorsal fin pterygiophores. An asterisk follows this measurement when it includes the depth of the dorsal fin pterygiophores.

Caudal peduncle depth = Vertical distance across tail immediately posterior to terminal dorsal and anal fin rays.

Caudal peduncle length = Medial horizontal distance from vertical through terminal dorsal and anal fin rays to posterior margin of hypural elements.

Snout to pelvic fin origin = Horizontal distance from tip of snout to vertical through origin of right pelvic fin (left in *H. stomata*).

Larval specimens for each species were not available in sufficient numbers to clear and stain for complete data on meristics and sequence of ossification of bony elements. However, fin ray counts were made and tabulated on unstained specimens. A partial larval series of *P. verticalis*, our most abundant species, was cleared with KOH and stained with Alizarin Red-S by Hollister's method (1934) to determine the process of axial skeletal development and fin formation. In addition, several larvae of *P. coenosus* and *P. decurrens* were cleared and stained for precaudal and

total vertebral counts which verified identifications and proved that Budd (1940) confused identifications of larvae of these two species. Radiographs of transforming larvae, juveniles, and adults of each species provided additional meristic data.

We divide the larval period into three stages, preflexion, flexion, and postflexion, based on the flexion of the notochord which occurs during caudal fin formation (Moser and Ahlstrom 1970; Ahlstrom et al. 1976; Moser et al. 1977). In *Pleuronichthys* and some other flatfishes the initiation of caudal fin formation begins while the notochord is still straight, in the late preflexion stage; we designate this phase as "early caudal formation." We found it convenient to divide the flexion stage into three substages, early flexion, midflexion, and late flexion, dependent upon the state of flexion of the notochord. In the early flexion stage, the notochord is very slightly flexed upward; in midflexion, it is flexed midway (nearly a 45° angle); and in late flexion, the notochord is approaching a terminal position, except that the caudal rays remain in a slightly oblique position. Transformation from the larval to juvenile stage was marked by eye migration, development of ossified pectoral fin rays, scales, and the lateral line.

MERISTIC COUNTS OF LARVAE

Meristic counts overlap among species considered here, and for discrimination of species it is necessary to use a combination of counts (Table 1). Precaudal and caudal vertebral counts, used in conjunction with dorsal and anal fin counts, are of most use in relating larvae to juveniles or adults. Pelvic fin ray counts are six per side in all seven species and branchiostegal ray counts are seven per side. Pectoral fin counts cannot be made on larvae since ossified pectoral rays form at metamorphosis. Gill rakers are not fully formed during the larval period in the species described.

DESCRIPTION OF EGGS

Pleuronichthys spp.

Eggs of three *Pleuronichthys* species were first described by Budd (1940) who collected them in plankton hauls from Monterey Bay, Calif. Budd noted the hexagonal patterns on the chorions of *Pleuronichthys* eggs. This type of ornamentation of the egg shell is confined to *Pleuronichthys* among flatfishes, but similar polygonal sculpturing is found on eggs of the families Synodontidae (Sanzo 1915; Mito 1961) and Callionymidae (Holt 1893; Ehrenbaum 1905; Mito 1962) and in a more exaggerated form on eggs of the sternoptychid, *Maurolicus muelleri* (Sanzo 1931; Mito 1961), and the macrourid, *Coelorhynchus coelorhynchus* (Sanzo 1933). Eggs of the three species of *Pleuronichthys* described by Budd were strikingly different in size; his largest, *P. coenosus*, averaged 1.88 mm in diameter, his intermediate-sized egg, *P. decurrens*, 1.44 mm, and his smallest, *P. verticalis*, 1.07 mm. All had homogeneous yolk, and lacked an oil globule. Our work shows that Budd misidentified the two larger eggs and corresponding larvae; the one he called *P. coenosus* is *P. decurrens* and vice versa. Orton and Limbaugh (1953) described an egg with an hexagonal pattern on its chorion that possessed a single oil globule; they tentatively, but correctly, assigned it to *P. ritteri*. White (1977) illustrated a developing egg of *P. ritteri* from Newport Bay, Calif.

Information concerning egg diameters, presence or absence of an oil globule, and character of the chorion are given in Table 2 for six of the seven species treated in this paper. Egg diameters do not change noticeably with the duration of preservation, although some shrinkage is known at the initial time of preservation. There is no overlap in egg size for the three species of *Pleuronichthys* that lack an oil globule. Eggs of *P. decurrens* range from 1.84 to 2.08 mm; those of *P. coenosus*, from

TABLE 1.—Meristics of the seven species of flatfishes in the eastern North Pacific that have heavily pigmented larvae.¹

Species	Dorsal rays	Anal rays	Pectoral rays (eyed side)	Vertebrae			Total gill rakers	Caudal rays	
				Precaudal	Caudal	Total		Total	Branched
<i>Pleuronichthys decurrens</i>	67-81	46-55	10-14	14-15	24-26	38-41	9-12	19-21	12-15(13)
<i>P. coenosus</i>	66-78	44-56	9-12	12-13	24-26	37-39	11-15	18-20(19)	12-15(13)
<i>P. verticalis</i>	66-79	44-51	10-12	13	23-25	36-38	9-11	19-20	12-14(13)
<i>P. ocellatus</i>	62-74	44-53	10-12	12-13	22-24	34-36	10-14	19	12-15(13)
<i>P. ritteri</i>	62-72	43-52	9-11	12-13	22-24	34-36	12-17	18-19	13-14
<i>Hypsopsetta guttulata</i>	65-75	47-55	11-13	11-12	22-24	34-36	?+2(5-6)	19-20	13
<i>Hippoglossina stomata</i>	63-70	47-55	11-12	11	26-28	37-39	15-21	17½-18½	11-13

¹Meristics compiled in Table 1 are derived in part from literature, particularly Fitch (1963), Norman (1934), Townsend (1936), Clothier (1950), and Ginsburg (1952), and in part from our original counts. Where a range is given and one count is predominant, that count is italicized.

²Lower limb count only.

TABLE 2.—Measurements of eggs of *Pleuronichthys* species, *Hypsopsetta guttulata*, and *Hippoglossina stomata*, including *Synodus lucioceps* for comparative data.

Species	Character of chorion	No. of eggs measured	No. of samples	Egg diameters (mm)			Oil globule diameters (mm)		
				Range	Mean	SD	Range	Mean	SD
<i>Pleuronichthys decurrens</i>	Sculptured	41	28	1.84-2.08	1.97	0.058	—	—	—
<i>P. coenosus</i> (CalCOFI)	Sculptured	20	15	1.28-1.56	1.47	0.066	—	—	—
<i>P. coenosus</i> (King Harbor)	Sculptured	287	2	1.20-1.42	1.29	0.047	—	—	—
<i>P. verticalis</i>	Sculptured	188	19	1.00-1.16	1.09	0.040	—	—	—
<i>P. ritteri</i>	Sculptured	82	13	0.94-1.08	1.01	0.029	0.08-0.14	0.10	0.009
<i>Hypsopsetta guttulata</i>	Smooth	35	4	0.78-0.89	0.84	0.027	0.12-0.14	0.13	0.010
<i>Hippoglossina stomata</i>	Smooth	26	9	1.22-1.38	1.29	0.045	0.20-0.26	0.23	0.018
<i>Synodus lucioceps</i>	Sculptured	168	8	1.20-1.48	1.32	0.049	—	—	—

1.20 to 1.56 mm; and those of *P. verticalis*, from 1.00 to 1.16 mm. Although eggs of *P. ritteri*, ranging in diameter from 0.94 to 1.08 mm, fall within the size range of *P. verticalis*, they can be readily distinguished by the presence of a small oil globule, 0.08-0.14 mm in diameter. Eggs of *P. ocellatus* were unavailable.

Differences in mean diameter of *P. coenosus* eggs were noted by locality, with eggs taken in open waters off the coast having a larger mean diameter and standard deviation (Table 2, CalCOFI collections) than eggs sampled from the inlet of a small, shallow, manmade harbor near a power plant discharge (Table 2, King Harbor samples). Except that they are often slightly larger in size, early- and middle-stage eggs of *P. coenosus* are difficult to differentiate from *Synodus lucioceps* eggs. They can be separated, however, by careful examination of the size and arrangement of polygons on the chorion. The mean of the greatest distance across polygons (sample size = 200 polygons) on *P. coenosus* eggs is 0.035 mm in contrast to 0.047 mm for *S. lucioceps* eggs (Table 3). Furthermore, the polygons on *P. coenosus* eggs are more regular in arrangement than on *S. lucioceps* eggs (Figure 1). This more uniform compacting of smaller polygons on *P. coenosus* eggs versus a more random patterning of larger polygons on *S. lucioceps* eggs is visible under a light microscope, and will separate these eggs. Late-stage eggs are easily distinguished by the heavy pigmentation on the embryo of *P. coenosus* compared with the sparse pigment on

advanced *S. lucioceps* embryos, which also have a longer gut.

The arrangement of polygons on the chorion of eggs of the other three species of *Pleuronichthys* from the eastern Pacific is similarly uniform (Figure 2). The polygons are somewhat larger on the chorion of eggs of *P. decurrens* and *P. verticalis* than *P. coenosus*, averaging ca. 0.042 mm in both species (Table 3). Interestingly, Budd (1940) gave the identical value, 0.042 mm, for this measurement on eggs of these two species. The polygons are smaller on eggs of *P. ritteri*, averaging 0.030 mm.

The eggs of *P. cornutus* were described by Mito (1963) and Takita and Fujita (1964). Mito gave the egg diameters as 1.16-1.26 mm, the oil globule as 0.016-0.020 mm. Takita and Fujita gave similar measurements for the hexagonal meshes of 0.018 mm, but gave a smaller egg diameter of 1.03-1.11 mm.

Hypsopsetta guttulata

Orton and Limbaugh (1953) obtained running ripe eggs of *H. guttulata* by stripping ripe adults and obtained similar eggs from plankton collections. The eggs were notable in that they contained a conspicuous, moderately large oil globule. This was the first record of an oil globule in eggs of flatfishes of the family Pleuronectidae, subfamily Pleuronectinae. The egg capsule was simple, without polygonal sculpturing or other apparent texture; the yolk was homogenous. Orton (1953) gave a fairly detailed description of pigment development on embryos of *H. guttulata*. Neither of the above papers contained information on egg size. Eldridge (1975) reported a mean egg diameter of 0.80 mm with usually one oil globule of 0.14 mm in mean diameter and numerous other small oil globules in the yolk. Eggs in our samples had a mean diameter of 0.84 mm (range 0.78-0.89 mm) with a single oil globule averaging 0.13 mm in

TABLE 3.—Comparison of polygon size on chorion of eggs of *Pleuronichthys* and *Synodus lucioceps*.

Species	No. of eggs measured	No. of polygons measured	Range of diameters (mm)	Mean (mm)	SD (mm)
<i>Synodus lucioceps</i>	20	200	0.038-0.053	0.047	0.0033
<i>Pleuronichthys coenosus</i>	20	200	0.029-0.043	0.035	0.0029
<i>P. decurrens</i>	2	20	0.038-0.046	0.042	0.0021
<i>P. verticalis</i>	2	20	0.037-0.051	0.042	0.0046
<i>P. ritteri</i>	2	20	0.028-0.032	0.030	0.0011

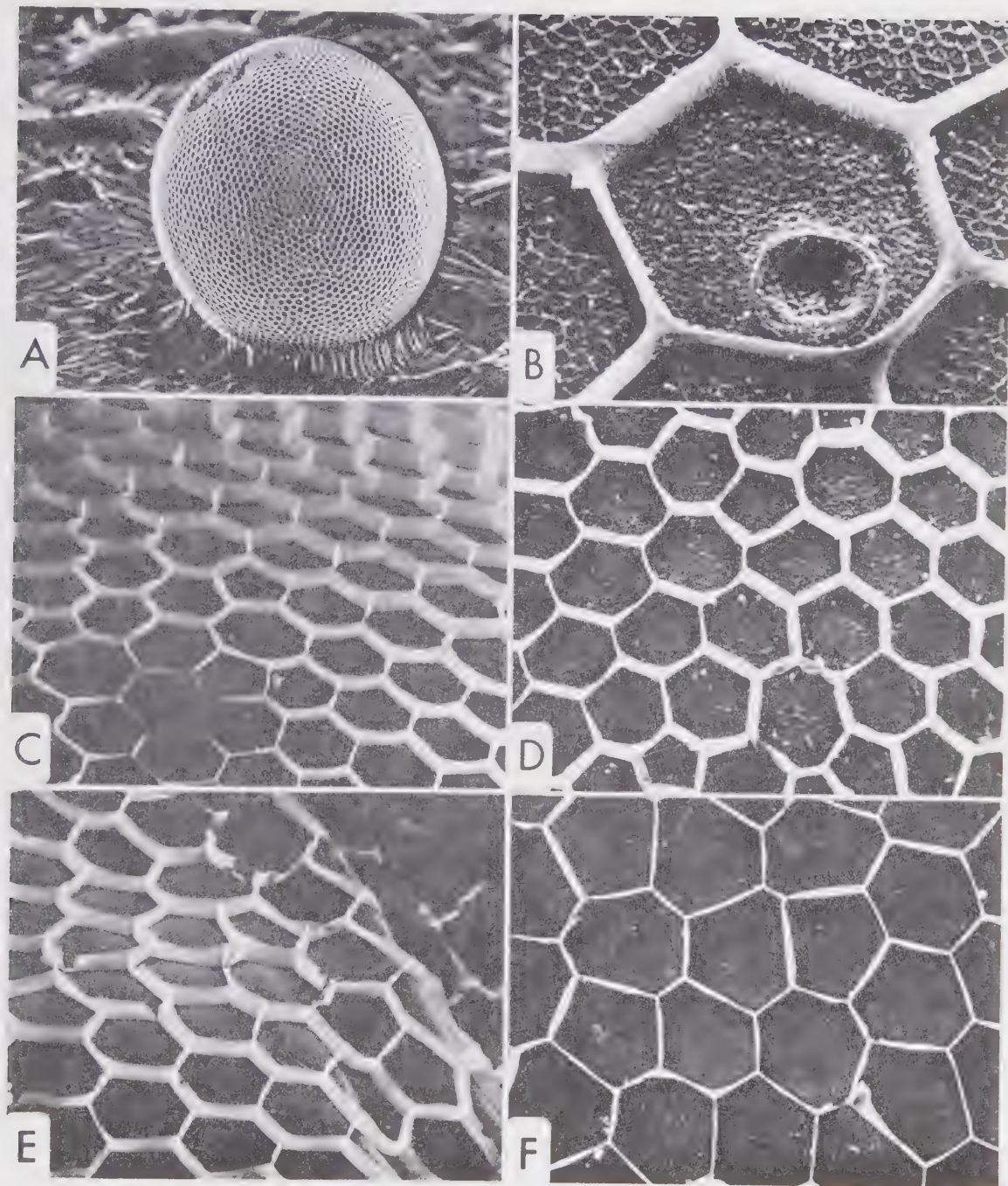


FIGURE 1.—Scanning electronmicrographs of *Pleuronichthys* and *Synodus luciocephalus* eggs. A. Entire egg of *P. coenosus*, 40 $\times$; B. Single polygon from same egg showing micropyle and texture of chorion surface, 1,880 $\times$; C. Side view of same egg showing polygons in perspective and micropyle at lower left, 420 $\times$; D. Face view of same egg, 480 $\times$; E. Side view of *S. luciocephalus* egg showing polygons in perspective, 455 $\times$; note delicate nature of polygons; F. Face view of same egg showing irregular nature of polygons and smooth surface of chorion, 490 $\times$.

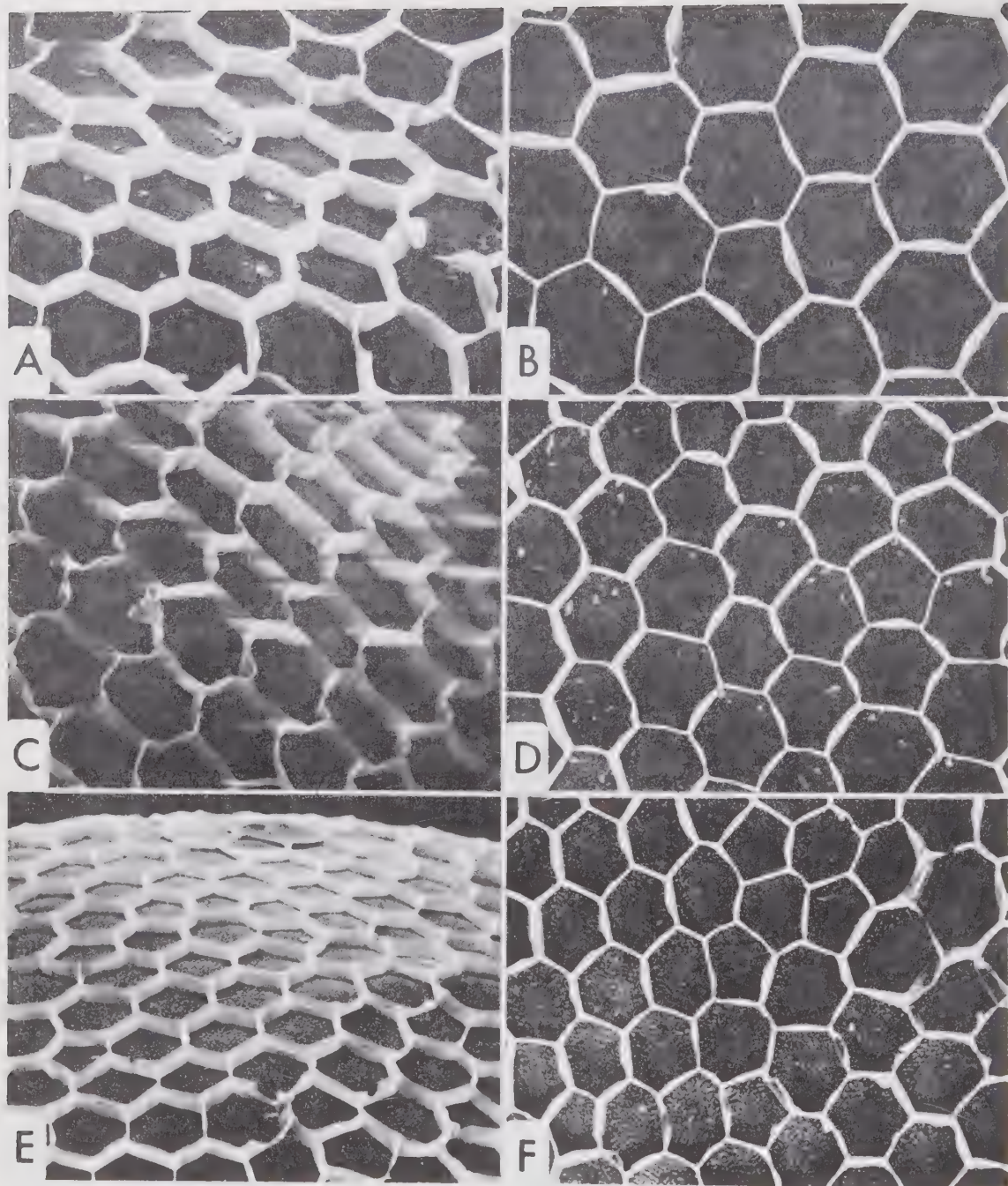


FIGURE 2.—Scanning electromicrographs of *Pleuronichthys* eggs. A. Side view of *P. decurrens* egg, 475 $\times$; B. Face view of same egg, 475 $\times$; C. Side view of *P. verticalis* egg, 410 $\times$; D. Face view of same egg, 450 $\times$; E. Side view of *P. ritteri* egg, 460 $\times$; F. Face view of same egg, 475 $\times$.

diameter (Table 2). There was no evidence of other small oil globules in the yolk, although a few eggs had a damaged oil globule which had separated in two. However, the original oil globule could easily be determined because of surrounding pigment. The oil globule is positioned near the center of the developing embryo in middle-stage eggs. The body of the late-stage embryo is heavily pigmented, similar to the newly hatched larvae.

Hippoglossina stomata

Eggs of *H. stomata* have not been previously described. Eggs are round with a slightly pinkish, unornamented shell and a single oil globule. The egg has a mean diameter of 1.29 mm (range 1.22–1.38 mm) and the oil globule a mean diameter of 0.23 mm (range 0.20–0.26 mm) (Table 2). The oil globule lacks pigment and lies near the tip of the tail of developing embryos in middle-stage eggs. In late-stage eggs the oil globule is in the posterior part of the yolk sac; the embryo is heavily pigmented over the body except for the posteriormost portion of the tail; pigment patches occur on the finfolds in the same places as in early preflexion stage larvae; pigment is widespread over the yolk surface.

DESCRIPTION OF DEVELOPMENTAL STAGES—LARVAL, TRANSFORMING, AND EARLY JUVENILE

Pleuronichthys decurrens Jordan and Gilbert (curlfin turbot) Figures 3, 4

Literature.—A series of egg stages and two preflexion larvae of *P. decurrens* were described and illustrated by Budd (1940) but incorrectly identified as *P. coenosus*. His larval illustrations were based on a recently hatched specimen, 5.54 mm, and an emaciated specimen, 8 days old, of somewhat smaller size.

Distinguishing characters.—Larvae of this species are unique in the genus *Pleuronichthys* in developing a pterotic spine on each side of the head, in having a higher precaudal vertebral number of 14 or 15, and in having the largest larvae during all stages of development. Larval pigmentation is heaviest in this species with the body and finfold entirely pigmented except for the posteriormost

region. Because of their relatively large size and dense pigment, *P. decurrens* larvae cannot be confused with *Hippoglossina stomata* or *Hypsopsetta guttulata*.

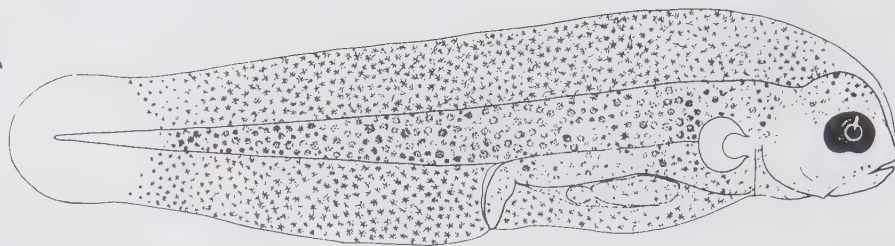
Pigmentation.—Newly hatched, preflexion, and early flexion larvae (4.9–9.8 mm NL) are heavily pigmented over the head, trunk, tail, and finfolds with only the pectoral fin and posteriormost tip of the notochord and finfold unpigmented (Figure 3A, B, C). As the first few caudal rays become evident (ca. 9.7 mm NL), several small, discrete melanophores appear on the pectoral fin base (Figure 3C). In late flexion and early postflexion stages during dorsal and anal fin development, the continuous heavy pigment on the finfolds changes to form three to four dorsal and three ventral bands of pigment which extend out from the body margin to part of the rayed fin membrane (Figure 3D). Larvae at this stage have a soft, saccular body with semitransparent and sparsely pigmented areas in the pterygiophore region between the body proper and developing dorsal and anal fins. Larvae >11.2 mm SL have dorsal and anal pterygiophores fully developed; the pterygiophore region is no longer transparent and the specimens become robust (Figure 4).

Morphology.—Larvae of *P. decurrens* are the largest members of the genus at hatching and attain the largest size before transformation. Our smallest specimen is 4.9 mm NL and has yolk remnants (Table 4). The left eye begins to migrate at 10.5 mm SL and has not completed migration in a larva 21.0 mm SL. The smallest available juvenile is 29.4 mm SL.

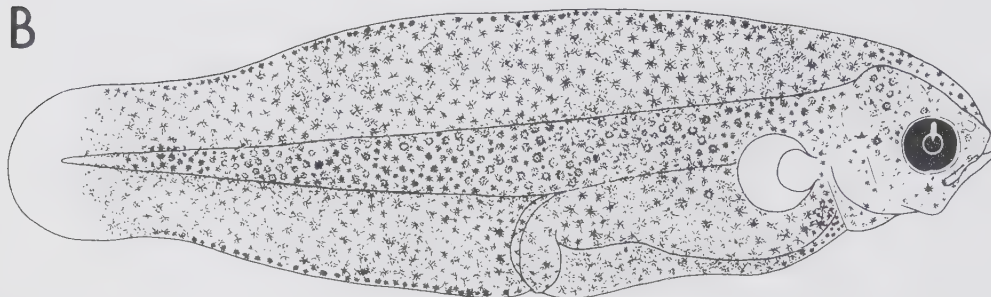
The gut begins as a tube which diminishes in diameter posteriorly and ends with a free terminal section that diverges from the body in a slight posteriad direction. In 5- to 7-mm NL larvae, the gut increases markedly in diameter and the free terminal section becomes vertical to the body axis. At about 8.0 mm NL, the gut begins to coil and its terminal section begins to slant anteriad. Coiling and the anterior displacement of the anus become more marked as development proceeds. This is reflected in the decreasing relative snout-anus length in postflexion larvae and especially in juveniles (Table 5).

Relative head length increases during larval development whereas relative snout length decreases (Table 5). Relative eye width decreases slightly during the three phases of the larval

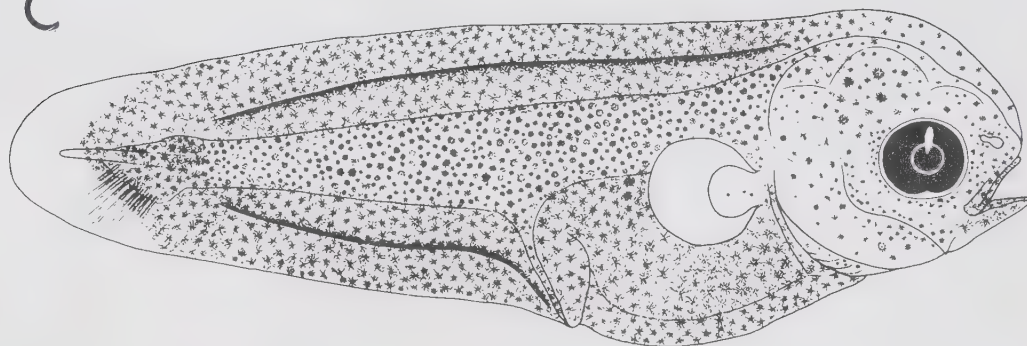
A



B



C



D

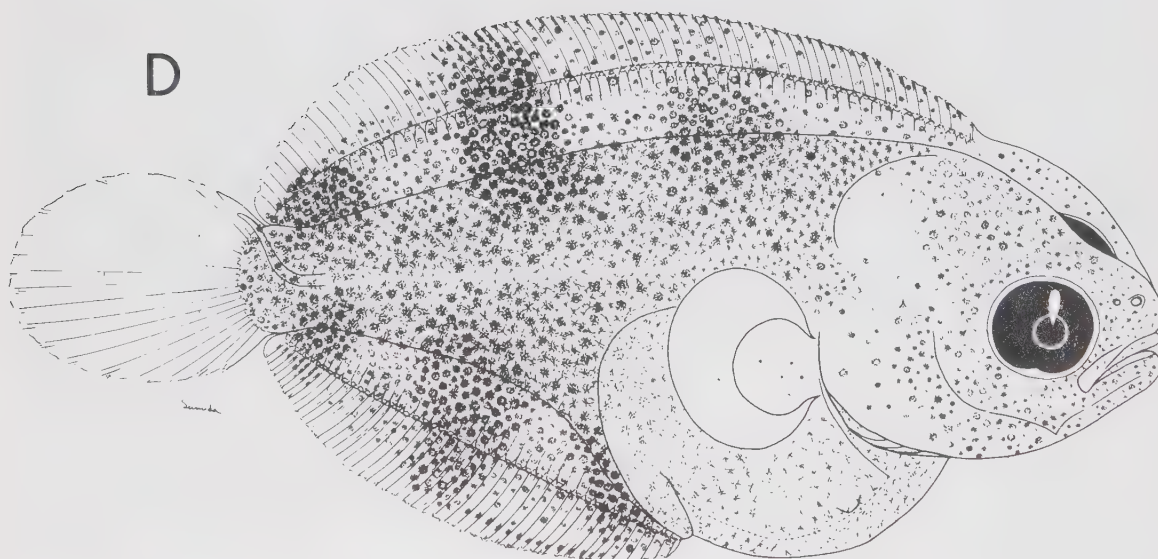
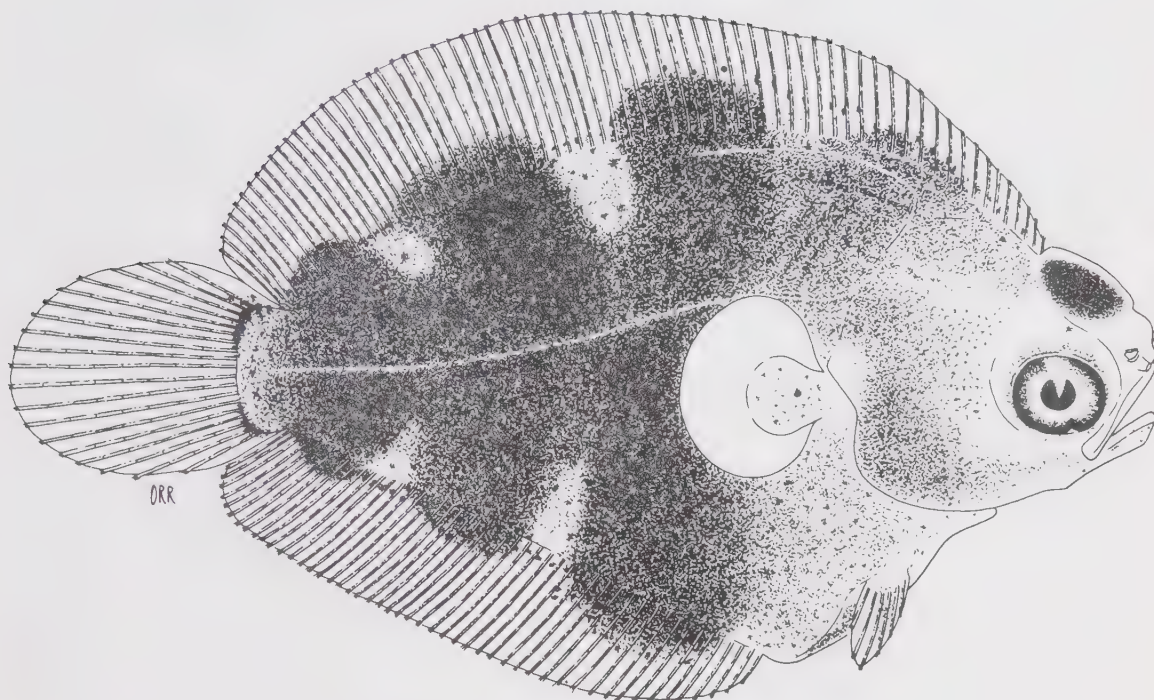


FIGURE 3.—Larval stages of *Pleuronichthys decurrens*: A. 5.9 mm; B. 6.5 mm; C. 9.7 mm; D. 10.0 mm.FIGURE 4.—Transforming specimen of *Pleuronichthys decurrens*, 14.4 mm.TABLE 4.—Morphometrics, in millimeters, of larvae and a juvenile of *Pleuronichthys decurrens*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye ¹	Notochord ²	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base ³	Body depth at anus ³	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5401-90.60	4.9 NL	Sym.	Str.	2.4	0.80	0.14	0.30	0.24	0.54	0.64	—	—	—
5704-87.50	5.6	Sym.	Str.	3.0	1.1	0.20	0.40	0.32	0.90	0.96	—	—	—
6501-63.52	6.0	Sym.	Str.	3.0	1.1	0.20	0.40	0.36	0.90	0.74	—	—	—
5206-70.65	6.5	Sym.	Str.	3.2	1.2	0.22	0.42	0.40	0.94	1.1	—	—	—
6501-60.70	7.9	Sym.	Str.	3.9	1.6	0.30	0.50	0.48	1.3	1.3	—	—	—
5003-87.35	8.5	Sym.	Str.	4.1	1.8	0.32	0.60	0.56	1.7	1.8*	—	—	—
6606-60.65	9.3	Sym.	Str.	4.3	2.0	0.32	0.66	0.62	1.6	1.8*	—	—	—
6605-80.80	9.8	Sym.	Str.	4.3	2.2	0.36	0.68	0.64	2.0	2.2*	—	—	—
5706-93.65	7.8	Sym.	E fl.	3.9	1.9	0.30	0.64	0.64	2.3*	2.3*	—	—	—
5711-87.55	9.1	Sym.	E fl.	4.7	2.1	0.40	0.70	0.66	2.4*	2.5*	—	—	—
5401-85.60	10.0	Sym.	Midfl.	4.4	2.6	0.44	0.80	0.72	2.8*	3.0*	—	—	2.7
6507-87.55	11.0	Sym.	L fl.	5.8	3.2	0.48	0.98	1.0	4.0*	4.6*	—	—	3.3
5009-47.60	10.2 SL	Sym.	Flexed	5.3	3.4	0.60	0.96	0.94	4.5*	4.6*	1.0	0.60	3.4
5407-60.70	10.5	Migr.	Flexed	5.5	3.6	0.64	1.1	1.1	4.9*	5.4*	1.0	0.64	3.4
5805-70.80	11.2	Migr.	Flexed	5.7	3.9	0.64	1.3	1.2	5.2*	5.9*	1.3	0.68	3.6
7505-90.70	14.5	Migr.	Flexed	6.2	5.2	0.66	1.6	0.96	8.1*	8.6*	2.1	0.83	4.6
4903-82.57	15.4	Migr.	Flexed	7.0	5.7	0.67	1.8	1.7	9.0*	9.7*	2.1	1.1	4.7
6609-80.60	17.0	Migr.	Flexed	8.7	6.4	0.67	1.9	1.5	9.2*	11.4*	2.9	1.2	6.0
5308-73.60	19.2	Migr.	Flexed	7.7	6.5	0.91	1.7	1.5	10.0*	11.4*	2.8	1.2	6.4
5004-97.32	21.0	Migr.	Flexed	8.4	6.7	0.66	1.7	1.7	11.7*	12.4*	3.2	1.4	6.2
Off Santa Cruz Island, Calif.	29.4	Over	Juv.	9.7	9.0	0.66	3.3	2.5	13.9*	14.5*	3.6	2.2	6.8

¹Sym. - symmetrical; Migr. - migrating.²Str. - straight; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Juv. - juvenile.³Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

TABLE 5.—Body proportions of larvae and early juveniles of seven flatfishes with heavily pigmented larvae. (Values given for each body proportion expressed as percentage of body length or head length: mean, standard deviation, and range. Numbers derived from data in morphometric tables for each species.)

	<i>Plurionichthys decurrens</i>	<i>P. coenosus</i>	<i>P. verticalis</i>	<i>P. ocellatus</i>	<i>P. ritteri</i>	<i>Hypoglossina guttulata</i>	<i>Hypoglossina stonata</i>
Snout to anus/body length:							
Preflexion	48.6±2.9(44-54)	46.2±3.4(39-50)	50.9±1.2(50-53)	—	49.2±3.8(44-57)	50.0±1.2(48-52)	40.1±3.9(36-45)
Flexion	49.8±4.0(44-55)	44.5±3.3(42-51)	50.0±4.7(44-56)	—	49.0±1.4(48-51)	48.5±1.7(46-50)	39.4±1.4(37-41)
Postflexion	46.9±5.3(40-52)	42.4±4.6(37-49)	42.7±4.3(36-45)	47.5±0.7(47-48)	40.7±7.9(31-51)	44.6±5.2(37-52)	40.5±2.6(36-44)
Juvenile	33	31	32.4±0.9(31-33)	32.2±2.2(30-36)	31.2±1.3(30-33)	36.0±1.1(35-38)	33.5±2.1(32-35)
Head length/body length:							
Preflexion	19.6±2.1(16-22)	20.0±2.7(15-23)	22.1±1.1(20-25)	—	24.4±2.3(20-28)	21.6±2.8(17-25)	21.5±3.3(17-26)
Flexion	25.5±2.6(23-29)	24.8±3.3(22-31)	27.3±1.9(25-30)	—	27.2±3.9(22-31)	25.8±1.3(24-27)	25.6±1.9(22-28)
Postflexion	34.9±2.0(32-38)	31.1±1.8(28-33)	33.2±2.6(31-37)	30.0	32.8±1.5(31-35)	33.0±1.9(30-36)	31.4±1.7(29-34)
Juvenile	31	28	27.4±1.5(26-30)	27.8±1.2(27-30)	29.0±1.2(28-30)	33.0±0.6(32-34)	34.5±0.7(34-35)
Snout length/head length:							
Preflexion	17.6±1.1(16-19)	20.5±3.5(16-27)	22.4±2.8(18-26)	—	18.8±1.8(17-22)	21.9±2.8(18-26)	18.1±4.0(10-24)
Flexion	16.8±1.7(15-19)	18.1±2.4(14-21)	19.7±3.1(15-23)	—	22.0±4.7(17-20)	18.8±1.5(17-20)	20.9±2.2(18-24)
Postflexion	13.9±3.2(10-18)	16.7±2.1(13-19)	14.7±2.9(11-18)	17.0±2.8(15-19)	16.3±1.4(15-18)	17.9±1.6(16-20)	23.1±2.8(19-27)
Juvenile	7	12	5.2±3.0(2-10)	14.2±1.5(12-16)	10.8±1.0(10-12)	14.7±1.8(12-17)	19.5±0.7(19-20)
Eye width/head length:							
Preflexion	34.1±2.5(31-38)	36.6±4.1(31-43)	36.4±4.1(31-44)	—	37.2±6.0(31-48)	40.6±3.1(37-45)	35.1±4.9(28-44)
Flexion	32.0±1.5(31-34)	32.0±2.6(28-35)	32.5±1.0(31-34)	—	33.5±6.4(29-43)	31.8±1.0(31-33)	31.9±1.5(30-34)
Postflexion	29.5±2.9(25-33)	29.6±1.7(26-31)	32.5±4.5(29-41)	28.5±2.1(27-30)	30.8±1.2(30-32)	31.5±2.7(28-36)	30.5±2.2(27-34)
Juvenile	37	30	38.4±3.0(34-42)	33.3±2.2(31-37)	36.2±2.9(32-38)	30.7±3.7(28-38)	33.0±2.8(31-35)
Eye height/head length:							
Preflexion	30.8±1.6(29-33)	32.1±2.0(29-35)	32.6±4.2(26-39)	—	32.8±3.9(29-40)	33.6±2.6(32-37)	28.6±3.4(26-33)
Flexion	31.0±2.4(28-34)	29.0±3.3(24-34)	30.8±1.7(28-33)	—	32.2±4.6(27-40)	28.8±1.5(27-30)	30.8±3.8(26-37)
Postflexion	26.1±4.7(18-31)	26.7±1.4(25-28)	27.0±2.8(23-30)	27.5±0.7(27-28)	27.2±2.2(25-31)	25.5±1.8(22-28)	29.4±3.1(24-36)
Juvenile	28	—	29.6±4.1(23-33)	33.3±2.2(31-37)	28.3±2.1(26-30)	24.2±3.4(21-30)	—
Body depth at P base before development of D base/body length:							
Preflexion	16.1±3.0(11-20)	17.4±4.5(8-22)	16.7±3.7(9-20)	—	20.9±6.4(10-28)	18.6±7.3(8-25)	17.6±4.5(12-23)
Flexion	23	—	—	—	—	23.2±1.0(22-24)	—
Body depth at P base after development of D base/body length:							
Preflexion	—	—	—	—	35	—	28.1±6.1(22-34)
Flexion	—	27.4±4.0(22-33)	29.8±3.1(25-33)	—	33.8±2.6(31-36)	—	30.6±2.1(28-33)
Postflexion	51.6±5.3(44-58)	39.9±5.9(31-45)	39.7±5.0(31-46)	33.0	40.7±1.5(39-42)	39.2±6.2(33-47)	38.1±2.0(36-41)
Juvenile	47	46	40.4±0.9(39-41)	42.0±1.6(39-43)	39.5±2.1(37-42)	52.8±1.5(51-54)	37.0
Body depth at anus before development of D&A bases/body length:							
Preflexion	15.0±2.4(12-17)	15.7±2.9(12-19)	14.3±0.8(13-15)	—	18.0±2.4(14-20)	18.4±3.4(13-22)	14.6±3.9(9-21)
Flexion	—	—	—	—	—	22.2±0.5(22-23)	—
Body depth at anus after development of D&A bases/body length:							
Preflexion	20.7±1.5(19-22)	28.3±4.2(24-35)	27.7±4.1(21-32)	—	27.7±5.5(22-33)	—	26
Flexion	32.5±6.4(28-42)	44.1±7.1(32-50)	41.7±5.8(31-46)	—	33.2±4.4(27-36)	—	26.6±2.6(24-31)
Postflexion	57.0±7.0(45-67)	49	42.2±0.8(41-43)	33.0	42.2±1.6(40-45)	41.2±6.1(35-48)	38.0±4.4(33-45)
Juvenile	49	—	—	44.8±1.7(42-47)	40.8±1.9(38-42)	54.7±1.2(54-57)	36.0
Caudal peduncle depth/body length:							
Preflexion	13.4±2.5(10-17)	12.4±2.4(9-16)	11.8±1.9(8-13)	7.5±0.7(7-8)	12.0±1.8(9-14)	9.1±1.4(8-11)	8.9±0.8(8-10)
Postflexion	—	14	13.2±0.8(12-14)	12.5±0.6(12-13)	11.5±0.6(11-12)	11.5±0.6(11-12)	9.5±0.7(9-10)
Juvenile	12	—	—	—	—	—	—
Caudal peduncle length/body length:							
Preflexion	6.4±0.5(6-7)	5.1±0.4(5-6)	6.5±1.2(5-8)	6.5±0.7(6-7)	5.8±0.5(5-7)	8.5±0.5(8-9)	8.5±0.5(8-9)
Postflexion	—	6	6.6±0.6(6-7)	6.3±0.5(6-7)	6.2±1.0(5-7)	8.0±1.1(6-9)	8.5±0.7(8-9)
Juvenile	7	—	—	—	—	—	—
Snout to pelvic base/body length:							
Preflexion	—	—	—	—	26	—	—
Flexion	28.5±2.1(27-30)	22.8±2.4(20-27)	26.2±1.8(25-29)	—	29.5±1.9(25-29)	24.4±1.8(22-27)	24.4±1.8(22-27)
Postflexion	32.1±1.6(30-35)	28.6±0.8(28-30)	28.6±3.1(24-32)	29.5±0.7(29-30)	29.3±3.9(26-36)	29.8±1.9(26-32)	28.0±2.6(24-30)
Juvenile	23	22	24.4±1.1(23-26)	23.8±1.3(22-26)	25.0±2.2(22-27)	27.8±0.8(27-29)	29.5±0.7(29-30)

period and then increases sharply in juveniles (Table 5). Relative eye height is consistently less than eye width; this is the usual pattern among all species being dealt with in this report.

The spine on each pterotic bone first appears on larvae about 6.0 mm NL and achieves maximum development in flexion larvae. It begins to regress near the end of the larval period and is a rugose bump in newly transformed juveniles. No other species of *Pleuronichthys* develops pterotic spines during the larval period, although they are present on larvae of *H. guttulata*.

Another distinctive feature of *P. decurrens* larvae is body depth. As in other species of *Pleuronichthys*, early larvae are slender. Relative body depth increases markedly during the postflexion stage with the result that larvae of this species become strikingly deeper bodied than those of the other six flatfishes with heavily pigmented larvae (Table 5).

Fin and axial skeleton formation.—Because this species is larger at corresponding stages of development than the other six flatfishes considered, fin formation occurs at comparatively larger larval sizes. Caudal fin development occurs between 7.9 and 11.0 mm NL; the smallest postflexion specimen, 10.2 mm SL, has the full count of 19 caudal rays (Table 6). The dorsal and anal fins begin forming simultaneously with the caudal, but obtain their full complement of rays later, by

14.5 mm SL. Pelvic buds are evident on most specimens undergoing flexion, but the full count of fin rays was first obtained on a 15.4-mm SL specimen. The axial skeleton is ossified on specimens as small as 11.2 mm SL, as determined by radiographs. Counts of 14 precaudal and 24-27 caudal vertebrae were recorded on five postflexion specimens.

Transformation.—Flatfish larvae are normally symmetrical larvae with eyes opposite each other on either side of the head during their preflexion to flexion stages and into the postflexion stage. Some flatfish larvae remain symmetrical with regard to eye placement until attaining quite large sizes, i.e., 50-120 mm (Hubbs and Chu 1934; Bruun 1937; Nielsen 1963; Amaoka 1970, 1971, 1972, 1973). However, in the flatfishes being studied the migration of one eye (left in dextral flounders, right in sinistral flounders) begins early in the postflexion stage. It can require some time to move completely over. Thus, the left eye was migrating on a 10.5-mm larva of *P. decurrens*, but was not completely over on a 21.0-mm specimen. Ossified rays are not formed in the pectoral fin until after eye migration is completed. On first formation the rays are spaced some distance apart in the blade of the pectoral fin. The pectoral fin rapidly changes form with the structure of the larval pectoral (base and blade) disappearing, to be replaced by a group of ossified, closely spaced rays. Metamorphosis is

TABLE 6.—Meristics of larvae and a juvenile of *Pleuronichthys decurrens*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage ¹	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
5401-90.60	4.9 NL	Prefl.	0	0	0	0	LP ²				
5704-87.50	5.6	Prefl.	0	0	0	0	LP ²				
6501-63.52	6.0	Prefl.	0	0	0	0	LP ²				
5206-70.65	6.5	Prefl.	0	0	0	0	LP ²				
6501-60.70	7.9	Prefl.	0	0	0	0	LP ²				
5003-87.35	8.5	Prefl.	Forming	Forming	Forming	0	LP ²				
6606-60.65	9.3	Prefl.	Forming	Forming	4	0	LP ²				
6605-80.80	9.8	Prefl.	Forming	Forming	ca. 8	0	LP ²				
5706-93.65	7.8	E fl.	Forming	Forming	ca. 8	Bud	LP ²				
5711-87.55	9.1	E fl.	Forming	Forming	ca. 12	0	LP ²				
5401-85.60	10.0	Midfl.	Forming	Forming	ca. 12	Bud	LP ²				
6507-87.55	11.0	L fl.	ca. 50	ca. 42	17	Bud	LP ²				
5009-47.60	10.2 SL	Postfl.	>50	46	19	Bud	LP ²				
5407-60.70	10.5	Postfl.	ca. 64	45	19	5/5	LP ²				
5805-70.80	11.2	Postfl.	71	46	19	5/5	LP ²	14	25	39	X-ray
7505-90.70	14.5	Postfl.	74	52	19	5/5	LP ²				
4903-82.57	15.4	Postfl.	72	48	19	6/6	LP ²	14	25	39	X-ray
6609-80.60	17.0	Postfl.	77	48	19	6/6	LP ²	14	24	38	X-ray
5308-73.60	19.2	Postfl.	75	52	19	6/6	LP ²	14	27	41	X-ray
5004-97.32	21.0	Postfl.	74	48	19	6/6	LP ²	14	25	39	X-ray
Off Santa Cruz Island, Calif.	29.4	Juv.	78	52	19	6/6	11/11	14	26	40	X-ray

¹Prefl. - preflexion; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.

²LP refers to functional larval pectoral fins which have no ossified rays.

considered complete when the lateral line can be discerned and scale formation has begun.

Distribution.—Fitch (1963) reported that the range for this species was from Alaska to San Quintin, Baja California. Miller and Lea (1976) gave an extended southern range limit to 25 mi north-northeast of Cedros Island (lat. $28^{\circ}47.5'N$, long. $114^{\circ}57.0'W$). Egg and larval material in our collections was taken off the entire coast of California over a broad band of stations, from nearshore to 150 or more miles offshore (Figure 5). Lack of egg and larval material off Baja California, despite the intensive coverage of these waters by CalCOFI surveys, indicates a more northerly distribution for young stages than for adults.

Pleuronichthys coenosus Girard
(C-O turbot)
Figures 6, 7

Literature.—Budd (1940) described and illustrated a series of eggs and four reared larvae of *P. coenosus* which he mistakenly identified as *P. decurrens*. The larvae illustrated were newly hatched to 9 days old, ranging in size from 3.88 to 4.72 mm.

Distinguishing characters.—This species is distinguished by having 13 (rarely 12) precaudal vertebrae and a total of 37-39 vertebrae. The larvae are larger than comparable stages of *H. guttulata* and other species of *Pleuronichthys* except *P. decurrens*. Pigmentation patterns discussed below will also separate *P. coenosus* from other species treated in this work.

Pigmentation.—Preflexion larvae are characterized by having opposing, similar appearing, pigment clusters on the dorsal and ventral finfolds posterior to the anus, and by small melanophores dotting the margin of the otherwise unpigmented posterior tip of the tail (Figure 6A, B). The rest of the body is heavily pigmented, with the exclusion of the undifferentiated pectoral fin and the ventral half of the head.

Flexion (6.2-7.8 mm NL) and postflexion larvae (7.1-11.4 mm SL) show an increase anteriorly of the finfold pigment and an increase in pigmentation on the lower region of the head (Figure 6C, D, E). A distinctively narrow, unpigmented zone along the hypurals persists through late flexion specimens, but is subsequently pigmented in

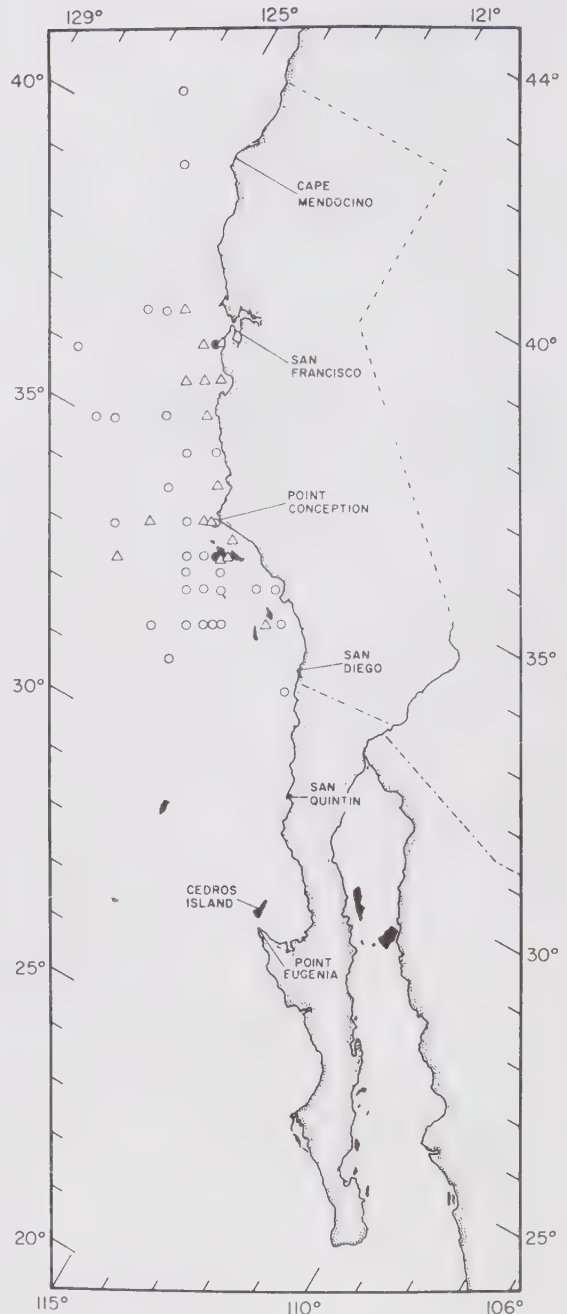
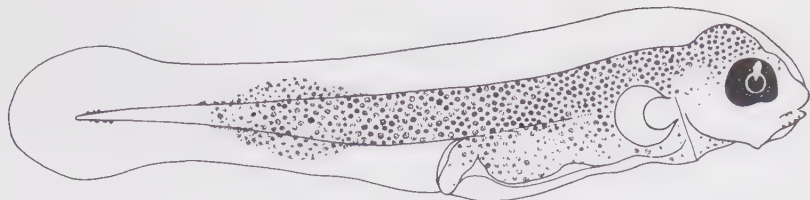


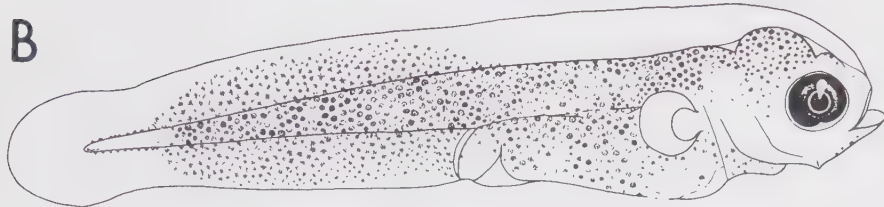
FIGURE 5.—Distribution of eggs and larvae of *Pleuronichthys decurrens* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

FIGURE 6.—Larval stages of *Pleuronichthys coenosus*: A. 3.7 mm; B. 5.9 mm; C. 6.1 mm; D. 7.8 mm; E. 8.9 mm.

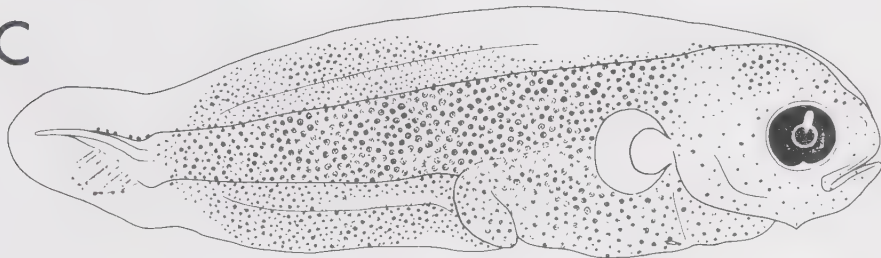
A



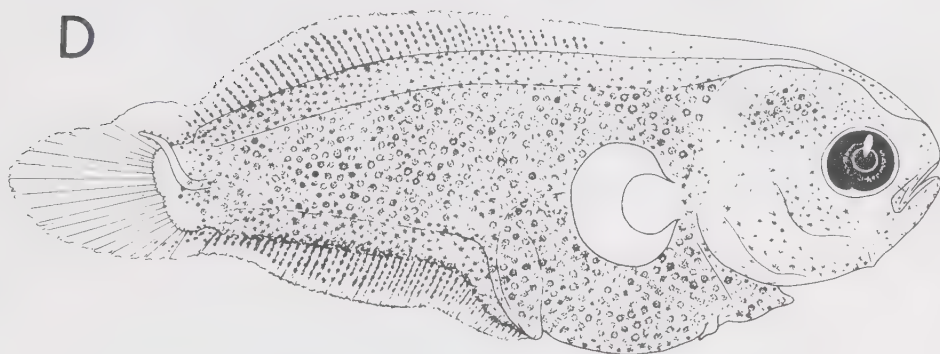
B



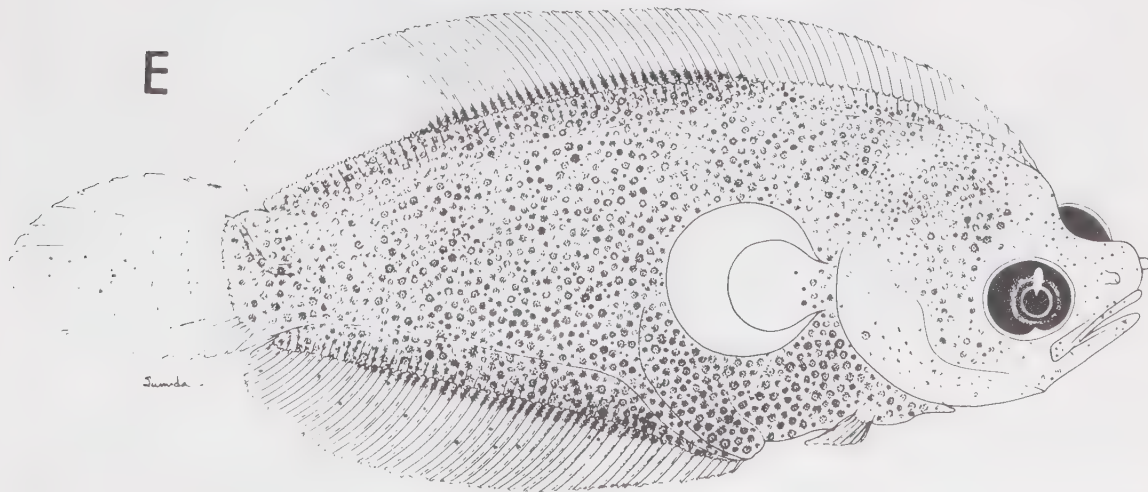
C



D



E



postflexion specimens (Figure 6E). A few pigment spots dot the anterior margin of the pectoral fin base in postflexion specimens, and extend farther onto the fin base in larger specimens. At dorsal and anal fin formation, pigment clustered in the finfold aligns along the dorsal and anal fin rays, and later in postflexion specimens becomes compacted into a narrow band adjacent to the fin bases. Pigment over the pterygiophores, however, is as dense as on the body (Figure 7).

Morphology.—Larvae of *P. coenosus* are larger at hatching and at transformation than all other species of *Pleuronichthys* except *P. decurrens*. A 3.9-mm NL specimen has much of its yolk sac remaining (Table 7). The smallest specimen in which the left eye begins to migrate is 8.2 mm SL; eye migration is almost complete in our largest transforming specimen, 11.4 mm SL.

The gut begins to coil and the free section becomes vertical to the body axis in larvae between 5.5 and 6.0 mm NL. Snout-anus distance has a moderate decrease relative to body length in all larval phases and decreases markedly after transformation (Table 5).

As in the other species, relative head length increases during larval development through the postflexion stage, but decreases moderately in juveniles. Both relative snout length and eye size decrease during the three larval phases (Table 5).

As in other species of *Pleuronichthys*, body depth increases during each larval stage (Table 5). Relative body depths for larvae of *P. coenosus* are in the intermediate range compared with other species in the genus. Body depth in juveniles is comparable with that in the relatively deep-bodied *P. decurrens*.

Fin and axial skeleton formation.—Fin formation in *P. coenosus* takes place at smaller sizes than in *P. decurrens* but at larger sizes than in other species of *Pleuronichthys*. Larvae undergoing caudal fin formation range from 6.2 to 8.5 mm NL. The smallest fully flexed larva is 7.1 mm SL. The full count of caudal rays is developed on a postflexion specimen 8.2 mm SL (Table 8). Dorsal and anal fin formation takes place at the same size as caudal fin formation; rays are mostly formed on late flexion specimens and fully formed on the 8.2-mm SL postflexion larva. Pelvic buds are present on all specimens undergoing notochord flexion except the smallest (6.2 mm NL), and the full count of six rays per fin is developed on the 9.6-mm SL postflexion specimen. Vertebral counts from two cleared and stained larvae, 8.6 and 10.0 mm SL, are 13+24.

Distribution.—Fitch (1963) denoted the distribution of *P. coenosus* as Alaska to Cape Colnett, Baja California. Collections of our egg and larval mate-

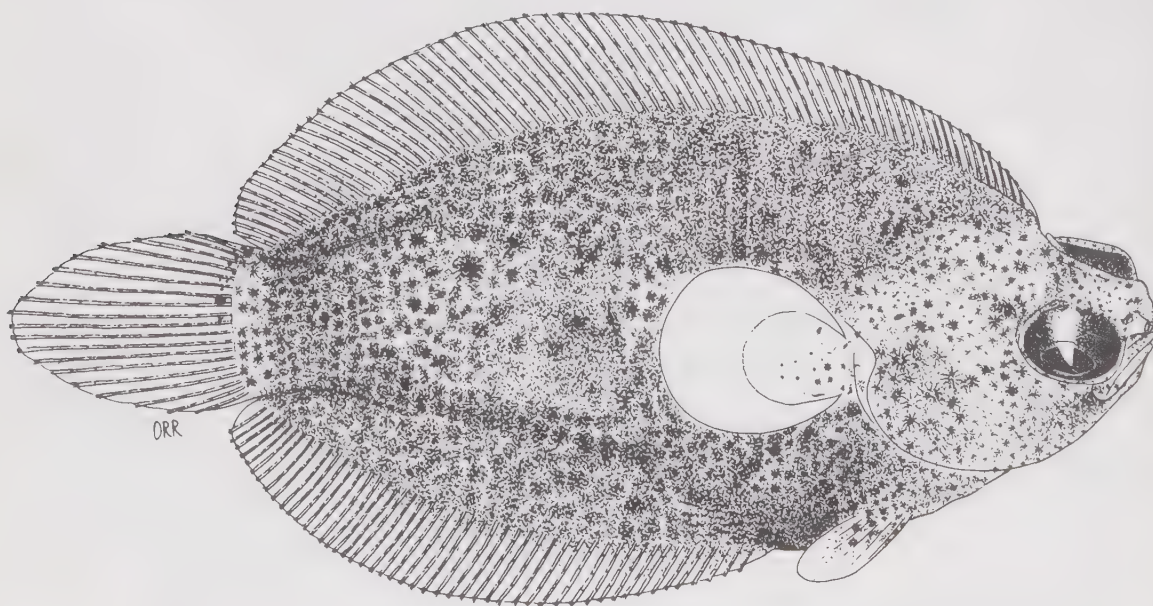


FIGURE 7.—Transforming specimen of *Pleuronichthys coenosus*, 10.0 mm.

TABLE 7.—Morphometrics, in millimeters, of larvae and a juvenile of *Pleuronichthys coenosus*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye ¹	Notochord ²	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base ³	Body depth at anus ³	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5902-83.43	3.9 NL	Sym.	Str.	1.8	0.60	0.16	0.26	0.20	0.30	0.46	—	—	—
5007-127.50	3.7	Sym.	Str.	1.8	0.68	0.14	0.26	0.22	0.60	0.52	—	—	—
5005-120.45	4.2	Sym.	Str.	2.1	0.80	0.16	0.32	0.24	0.70	0.56	—	—	—
Off La Jolla, Calif.	5.1	Sym.	Str.	2.5	1.1	0.20	0.40	0.38	1.1	0.90	—	—	—
5704-82.47	5.6	Sym.	Str.	2.6	1.1	0.26	0.40	0.36	0.90	0.84	—	—	—
6304-93.40	6.9	Sym.	Str.	3.1	1.6	0.30	0.50	0.46	1.3	1.3	—	—	—
6304-120.70	6.5	Sym.	Str.	3.0	1.5	0.28	0.46	0.46	1.4	1.6*	—	—	—
5206-90.41	8.5	Sym.	Str.	3.3	1.7	0.28	0.64	0.60	1.6	1.6	—	—	—
5110-97.30	6.2	Sym.	E fl.	2.7	1.4	0.30	0.48	0.42	1.4	1.5*	—	—	—
7207-93.45	7.2	Sym.	E fl.	3.1	1.6	0.30	0.56	0.54	1.6	1.8*	—	—	1.6
5705-93.27	7.4	Sym.	Midfl.	3.3	1.8	0.26	0.60	0.54	2.0*	1.9*	—	—	1.6
5304-85.50	8.3	Sym.	Midfl.	3.5	1.9	0.36	0.60	0.54	2.2*	2.4*	—	—	1.7
1941-25.45	7.2	Sym.	L fl.	3.1	1.9	0.36	0.58	0.54	2.1*	2.2*	—	—	1.6
4908-72.56	7.8	Sym.	L fl.	4.0	2.4	0.40	0.68	0.58	2.6*	2.7*	—	—	2.1
5007-90.53	7.1 SL	Sym.	Flexed	3.3	2.0	0.38	0.62	0.56	2.2*	2.3*	0.62	0.36	2.0
5004-100.60	8.2	Migr.	Flexed	3.4	2.5	0.40	0.74	0.70	3.1*	3.4*	0.98	0.50	2.3
6606-70.70	8.8	Migr.	Flexed	4.0	2.7	0.48	0.80	0.74	2.9*	3.3*	0.84	0.42	2.6
5304-85.50	9.6	Migr.	Flexed	4.7	3.0	0.60	0.92	0.80	4.2*	4.8*	1.2	0.52	2.8
5206-90.41	9.9	A. over	Flexed	3.9	3.2	0.56	0.84	0.80	4.4*	4.9*	1.4	0.48	2.8
5407-83.51	10.2	A. over	Flexed	3.8	3.4	0.52	1.0	0.84	4.6*	5.1*	1.6	0.52	3.0
5304-100.29	11.4	Over	Flexed	4.3	3.4	0.60	1.0	0.88	5.0*	5.4*	1.6	0.60	3.2
Off Coronados Islands, B.C.	17.0	Over	Juv.	5.2	4.7	0.58	1.4	—	7.9*	8.3*	2.4	1.0	3.8

¹Sym. - symmetrical; Migr. - migrating; A. over - About over.²Str. - straight; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Juv. - juvenile.³Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.TABLE 8.—Meristics of larvae and a juvenile of *Pleuronichthys coenosus*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage ¹	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
5902-83.43	3.9 NL	Yolk-sac	0	0	0	0	LP ²				
5007-127.50	3.7	Prefl.	0	0	0	0	LP ²				
5005-120.45	4.2	Prefl.	0	0	0	0	LP ²				
Off La Jolla, Calif.	5.1	Prefl.	0	0	0	0	LP ²				
5704-82.47	5.6	Prefl.	0	0	0	0	LP ²				
6304-93.40	6.9	Prefl.	0	0	0	0	LP ²				
6304-120.70	6.5	Prefl.	Forming	Forming	4	0	LP ²				
5206-90.41	8.5	Prefl.	Forming	Forming	ca. 8	0	LP ²				
5110-97.30	6.2	E fl.	Forming	Forming	ca. 8	0	LP ²				
7207-93.45	7.2	E fl.	Forming	Forming	12	Bud	LP ²				
5705-93.27	7.4	Midfl.	Forming	Forming	12	Bud	LP ²				
5304-85.50	8.3	Midfl.	Forming	30	12	Bud	LP ²				
1941-25.45	7.2	L fl.	ca. 55	ca. 44	ca. 14	Bud	LP ²				
4908-72.56	7.8	L fl.	ca. 60	ca. 45	16	Bud	LP ²				
5007-90.53	7.1 SL	Postfl.	ca. 70	ca. 50	16	Bud	LP ²				
5004-100.60	8.2	Postfl.	74	55	19	ca. 4/4	LP ²				
6606-77.55	8.6	Postfl.	72	54	19	ca. 5/5	LP ²	13	24	37	C&S ³
6606-70.70	8.8	Postfl.	76	50	19	ca. 4/4	LP ²				
5304-85.50	9.6	Postfl.	73	ca. 52	19	6/6	LP ²				
5206-90.41	9.9	Postfl.	69	50	19	6/6	LP ²				
5206-87.45	10.0	Postfl.	71	53	19	—	LP ²	13	24	37	C&S ³
5407-83.51	10.2	Postfl.	69	49	19	6/6	LP ²				
5304-100.29	11.4	Postfl.	72	50	19	6/6	LP ²				
Off Coronados Islands, B.C.	17.0	Juv.	75	53	19	6/6	9/9	13	25	38	X-ray

¹Prefl. - preflexion; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Post fl. - postflexion; Juv. - juvenile.²LP refers to functional larval pectoral fins which have no ossified rays.³Cleared and stained.

rial range from northern California south to Point Abrejos, Baja California (Figure 8). Our records extend the range considerably southward for the

species. Larval specimens range widely from nearshore to about 200 mi offshore, but most occurrences are between 50 and 200 mi offshore.

Pleuronichthys verticalis Jordan and
Gilbert (hornyhead turbot)
Figures 9, 10

Literature.—The eggs and two early larvae (3.16 and 3.35 mm) were described and illustrated by Budd (1940). Four illustrations of larvae, between 4.4 and 8.7 mm SL, are contained in CalCOFI Atlas No. 23 (Ahlstrom and Moser 1975).

Distinguishing characters.—Preflexion and early flexion larvae of this species are recognizable by the triangular patches of pigment, one each on the dorsal and ventral finfold posterior to the anus; these form late in the yolk-sac stage and persist through the notochord flexion stage. No other species of *Pleuronichthys* develops this distinctive pigmentation character.

Late flexion and postflexion larvae are distinguished by size (i.e., larger than *H. guttulata*, *P. ritteri*, and *P. ocellatus*, but smaller than *P. coenosus* and *P. decurrens*), and by sparse pigment on the head and on the dorsal and anal fin pterygiophores. This is in sharp contrast to the heavy pigment in these areas for the other species discussed.

Newly transformed specimens are difficult to distinguish from comparable stages of *P. ritteri*. However, pigment on the body tends to be mottled on *P. verticalis* rather than evenly distributed as on *P. ritteri* at this stage. Small juveniles are easily separable from *P. ritteri* because *P. verticalis* lacks the anterior prolongation of the supratemporal branch of the lateral line found on *P. ritteri* juveniles.

Pigmentation.—Pigment on yolk-sac and older preflexion larvae of *P. verticalis* is heavy on the head, trunk, and tail and ends anterior to the last three to five myomeres (Figure 9A, B). As the last remnant of yolk is absorbed, scattered finfold pigment differentiates into triangular-shaped clusters posterior to the anus, the dorsal patch being situated slightly anterior of the ventral patch. The head region below and on each side of the eye is only sparsely pigmented which is typical of most early preflexion larvae of several species of *Pleuronichthys*. The top of the head to the shoulder region is unpigmented, a character shared with preflexion larvae of *P. ritteri*. Small pigment spots dot the margin of the tip of the tail, but do not persist beyond the flexion stage (Figure 9C, D).

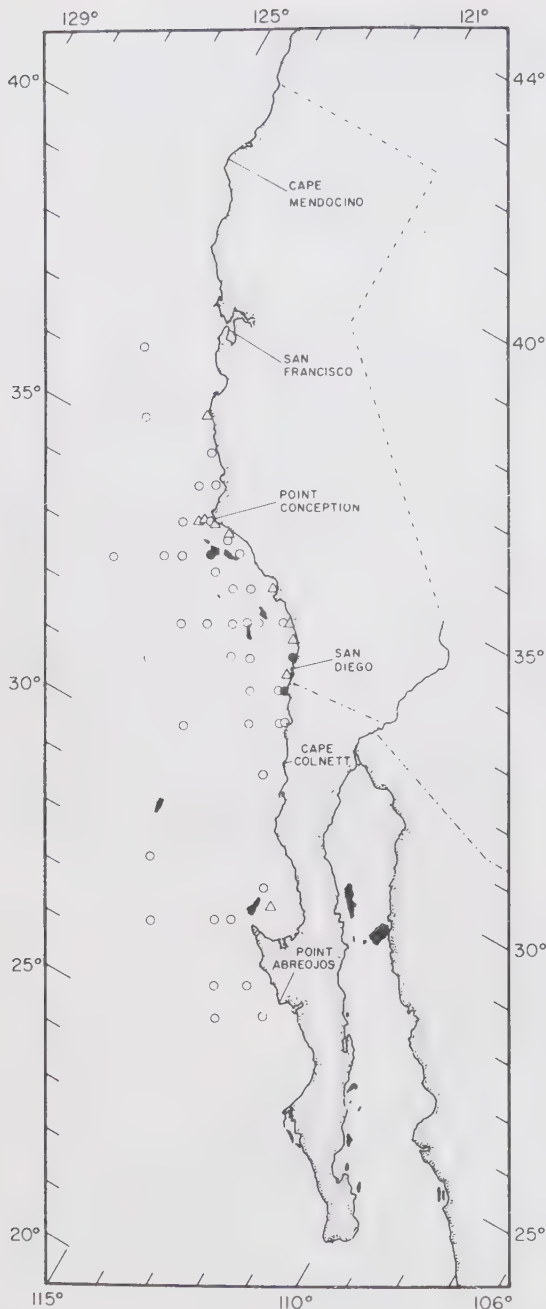


FIGURE 8.—Distribution of eggs and larvae of *Pleuronichthys coenosus* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

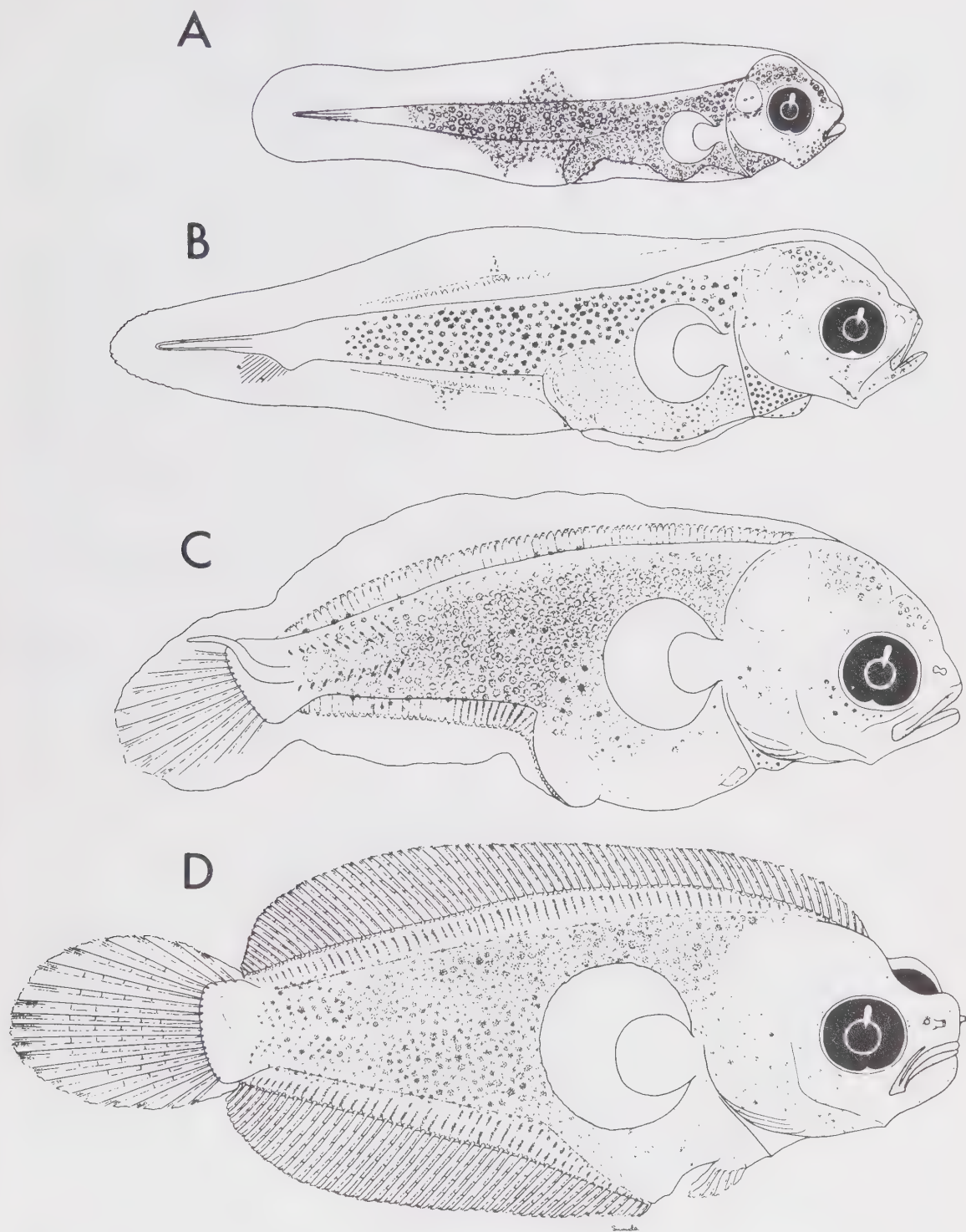


FIGURE 9.—Larval stages of *Pleuronichthys verticalis*: A. 4.4 mm; B. 6.5 mm; C. 7.1 mm; D. 8.7 mm.

Flexion larvae undergo little change in pigment pattern from earlier stages. The triangular patches of finfold pigment are diminished in size and pigment intensity, but are visible by careful examination in specimens through notochord flexion.

Following the completion of notochord flexion, pigment on the tail spreads posteriad leaving only the caudal peduncle unpigmented (Figure 9D). The outlying regions of the head and body, particularly the pterygiophore region, are sparsely pigmented compared with late larvae of other *Pleuronichthys* species and *H. guttulata*.

Transformed specimens develop heavy pigment over the body giving them a mottled appearance. Dark blotches appear along bases of the dorsal and anal fins (Figure 10).

Morphology.—Larvae of *P. verticalis* attain a size intermediate between the large species, *P. decurrens* and *P. coenosus*, and the smaller *P. ritteri*. A specimen with most of its yolk sac remaining is 2.4 mm NL (Table 9). The left eye is beginning to migrate in a specimen as small as 7.3 mm SL and transformation is almost complete at 9.2 mm SL. The smallest available juvenile is 12.2 mm SL, reared from eggs collected off San Diego, Calif.

Gut development follows the course of other *Pleuronichthys*. Snout-anus length is about 50% of body length in preflexion and flexion stages and

then is reduced in postflexion and early juvenile stages. The gut begins to coil at about 4.0 mm NL but the free terminal section does not become vertical until at least 5.0 mm NL.

As in the other species, relative head length increases throughout the larval period and then decreases at transformation. Snout length and eye size undergo a gradual relative diminution during the larval stages; however, relative eye width increases sharply at transformation (Table 5).

Larvae of *P. verticalis* are intermediate in body depth when compared with other species of *Pleuronichthys* (Table 5).

Fin and structural development.—*P. verticalis* is the only species for which we could clear and stain a series of larvae (Tables 10, 11). The sequence of fin formation was followed more precisely in this species as was the sequence of ossification of other structures including the vertebral column, supporting bones of the caudal fin, branchiostegal rays, gill rakers, and teeth.

The caudal fin begins to form on the under side of the body a short distance anterior to the tip of the notochord on specimens of about 5.0 mm NL. Some caudal rays form before flexion begins (Figure 11A). Rays initially form at midcaudal and those that will be associated with superior hypural bones differentiate posteriorward, while those that will be associated with inferior hypural bones

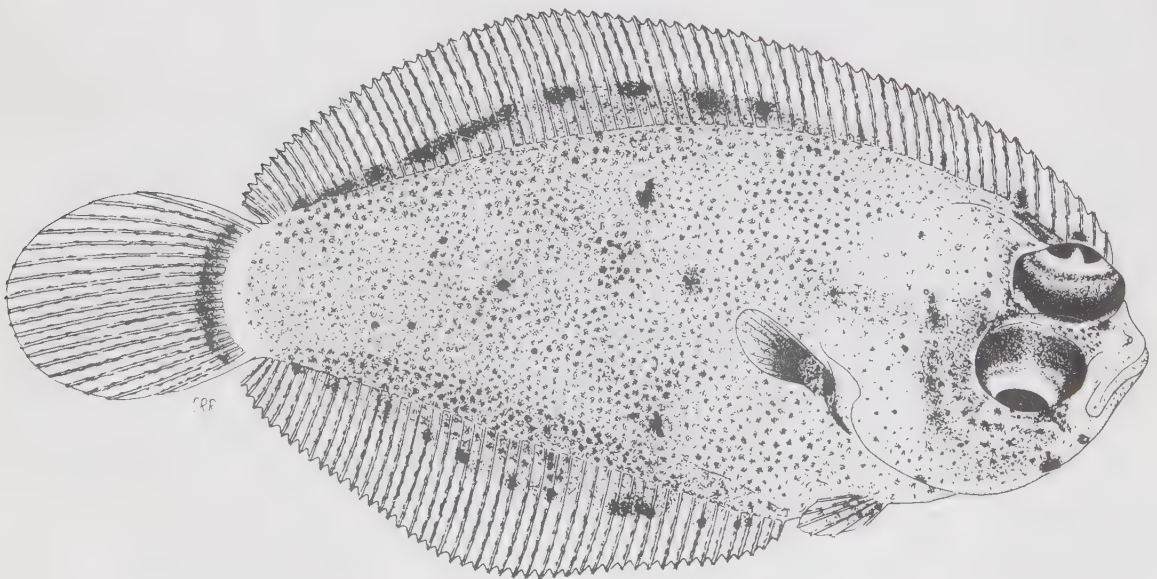


FIGURE 10.—Reared transforming specimen of *Pleuronichthys verticalis*, 11.0 mm.

TABLE 9.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys verticalis*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye ¹	Notochord ²	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base ³	Body depth at anus ³	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
7501-120.26 Off La Jolla, Calif.	2.4 NL	Sym.	Str.	1.2	0.56	0.10	0.22	0.20	0.22	0.34	—	—	—
SCBS-2-203	2.7	Sym.	Str.	1.4	0.54	0.12	0.24	0.22	0.38	0.40	—	—	—
7203-103.30	3.0	Sym.	Str.	1.5	0.64	0.16	0.22	0.20	0.48	0.40	—	—	—
7203-103.30	3.8	Sym.	Str.	2.0	0.86	0.20	0.30	0.26	0.70	0.54	—	—	—
7203-103.30	4.3	Sym.	Str.	2.2	0.94	0.24	0.34	0.32	0.84	0.62	—	—	—
7203-103.30	4.8	Sym.	Str.	2.4	1.0	0.20	0.36	0.32	0.90	0.70	—	—	—
7501-120.26	5.2	Sym.	Str.	2.6	1.3	0.30	0.40	0.34	1.0	0.80	—	—	—
5708-110.33	5.0	Sym.	E fl.	2.8	1.5	0.34	0.50	0.42	1.6*	1.4*	—	—	—
7203-103.30	5.6	Sym.	E fl.	2.7	1.4	0.30	0.48	0.46	1.4*	1.2*	—	—	1.5
7503-90.27.6	5.6	Sym.	Midfl.	2.9	1.5	0.30	0.48	0.46	1.8*	1.8*	—	—	1.4
5510-117.26	5.9	Sym.	Midfl.	2.7	1.6	0.24	0.50	0.52	1.7*	1.6*	—	—	1.5
7503-120.26	7.2	Sym.	Midfl.	3.2	1.9	0.32	0.60	0.56	2.1*	2.0*	—	—	1.8
5708-110.33	6.3	Sym.	L fl.	3.2	1.9	0.32	0.60	0.56	2.1*	2.0*	—	—	1.8
7505-120.30	6.5 SL	Sym.	Flexed	3.2	2.0	0.36	0.64	0.60	2.0*	2.0*	0.54	0.50	?
SCBS-4-303	7.3	Migr.	Flexed	3.3	2.6	0.40	0.76	0.68	3.1*	3.3*	0.96	0.40	2.2
5506-120.45	7.9	Migr.	Flexed	3.3	2.9	0.40	0.84	0.68	3.6*	3.6*	1.0	0.44	2.4
6606-103.29	8.3	Migr.	Flexed	3.5	2.7	0.48	0.84	0.68	3.2*	3.5*	1.0	0.44	2.7
6504-137.30	9.2	Migr.	Flexed	3.9	2.9	0.36	0.96	0.84	3.8*	4.2*	1.1	0.60	2.5
Reared	11.0	Over	Flexed	4.0	3.4	0.36	1.4	1.0	4.3*	4.4*	1.4	0.76	2.7
Reared	12.2	Over	Juv.	4.0	3.6	0.36	1.4	1.2	5.0*	5.1*	1.6	0.80	3.2
Reared	15.9	Over	Juv.	5.2	4.3	0.32	1.8	1.4	6.5*	6.6*	2.2	1.0	3.6
Reared	16.9	Over	Juv.	5.3	4.5	0.32	1.8	1.3	6.6*	6.9*	2.3	1.0	4.2
Santo Tomas	19.5	Over	Juv.	6.4	5.3	0.08	1.8	1.2	7.8*	8.4*	2.5	1.3	4.7
Bay, B.C.	26.5	Over	Juv.	8.4	7.0	0.33	2.6	2.1	10.9*	11.4*	3.3	1.9	6.5

¹Sym. - symmetrical; Migr. - migrating.²Str. - straight; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Juv. - juvenile.³Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.TABLE 10.—Meristics of larvae and juveniles of *Pleuronichthys verticalis*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage ¹	Fin ray						Teeth			
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Gill rakers	Upper jaw R	Lower jaw L	Upper jaw L	Lower jaw R
6609-97.29	5.3 NL	Prefl.	Forming	Forming	4	0	LP ²	—	—	—	—	—
7503-90.27.6	5.6	Prefl.	Forming	Forming	4	0	LP ²	—	—	—	—	—
—	5.5	Prefl.	Forming	Forming	6	0	LP ²	—	—	—	—	—
6507-107.30	5.8	Prefl.	Forming	Forming	6	0	LP ²	—	—	—	—	—
5708-117.26	5.7	Prefl.	Forming	Forming	6	0	LP ²	—	—	—	—	—
5708-117.26	5.8	Prefl.	Forming	Forming	6	0	LP ²	—	—	—	—	—
5708-117.26	6.1	E fl.	Forming	Forming	8	Bud	LP ²	—	—	—	—	—
—	7.0	L fl.	43	37	16	Bud	LP ²	0+2	1	2	3	3
6606-97.29	6.9	L fl.	63	43	18	4/4	LP ²	0+3	1	2	0	3
—	7.0	Postfl.	67	47	19	5/5	LP ²	0+6	1	3	3	5
6407-83.43	7.1	Postfl.	64	44	19	3/3	LP ²	Not taken	1	4	3	5
5110-100.40	7.3	Postfl.	67	47	19	5/5	LP ²	0+5	?	6	5	6
6606-97.29	8.3	Postfl.	65	46	19	6/6	LP ²	0+5	0	5	5	7
6504-137.30	9.2	Postfl.	65	44	19	6/6	LP ²	Not taken	—	—	—	—
Reared	11.0	Postfl.	72	49	19	6/6	11/7	2+9	—	—	—	—
Reared	12.2	Juv.	72	47	19	6/6	11/11	3+7	—	—	—	—
Reared	15.9	Juv.	74	49	20	6/6	12/12	3+8	—	—	—	—
Reared	16.9	Juv.	72	48	19	6/6	10/11	3+7	—	—	—	—
Santo Tomas	19.5	Juv.	67	47	19	6/6	10/10	2+7	—	—	—	—
Bay, B.C.	26.5	Juv.	70	49	19	6/6	11/11	3+7	—	—	—	—

¹Prefl. - preflexion; E fl. - early flexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.²LP refers to functional larval pectoral fins which have no ossified rays.

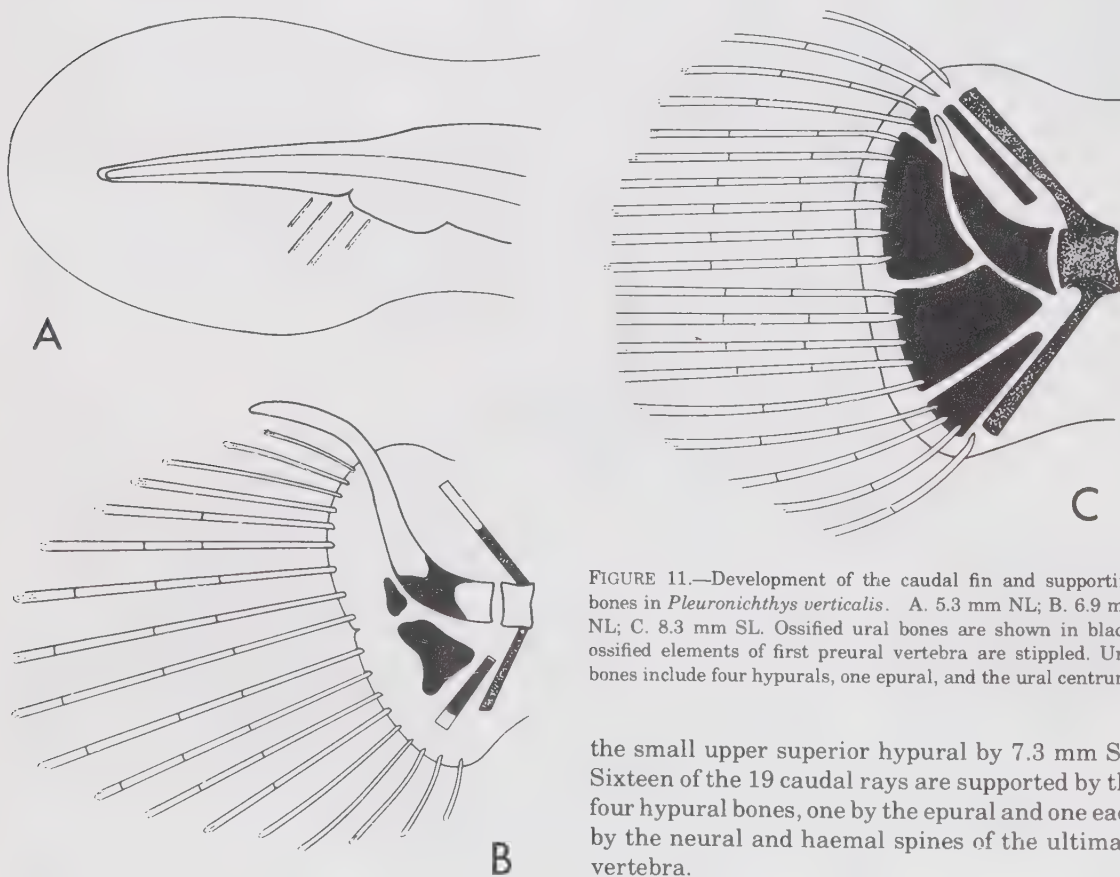
differentiate progressively anteriorward. A number of specimens, 5.3-5.8 mm NL with the notochord still straight, possess 2+2 or 3+3 caudal rays. The complete complement of 10+9 caudal rays is present on specimens 7.0 mm NL and larger. Flexion occurs in larvae between 6.1 and 7.0 mm NL (Figure 11B). By the time the

caudal ray complement is fully formed, the rays are aligned in a terminal position (Figure 11C). The hypurals are observed as cartilaginous plates before they ossify. There are two superior and two inferior hypurals³ in pleuronectid flatfishes. The

³We include the "parhypural" as a hypural bone. In flatfishes it is a splinter bone without remnant of a haemal arch.

TABLE 11.—Development of vertebral column, caudal fin rays, and caudal fin supporting bones in larvae of *Pleuronichthys verticalis*.

Station	Body length	Stage ¹	Precaudal vertebrae ²		Caudal vertebrae ²					Total vert. ³	C fin rays	Ural bones ²				Epural
			n.pr.	centra	n.pr.	h.pr.	centra	Ural centrum	Sup. hyp.			Inf. hyp.				
									Upper			Mid	Mid	Lower		
6609-97.29	5.3 NL	Prefl.	0	0	0	0	0	0	0	2+2	0	0	0	0	0	
7503-90.27.6	5.6	Prefl.	0	0	0	7	0	0	7*	2+2	0	0	0	0	0	
—	5.5	Prefl.	4+2	0	14	14	0	0	20*	3+3	0	0	0	0	0	
6507-107.30	5.8	Prefl.	6+3	0	15	15	0	0	24*	3+3	0	0	0	0	0	
5708-117.26	5.7	Prefl.	7+5	0	16	16	0	0	28*	3+3	0	0	0	0	0	
6507-107.30	5.8	Prefl.	7+4	0	17	17	0	0	28*	3+3	0	0	0	0	0	
5708-117.26	6.1	E fl.	13	0	19	20	0	0	33*	4+4	0	0	0	0	0	
—	7.0	L fl.	13	0	22	22	0	0	35*	8+8	0	0	0	0	0	
6606-97.29	6.9	L fl.	13	13	22	22	20	1	36	9+9	0	X	X	X	0	
—	7.0 SL	Postfl.	13	13	23	23	23	1	37	10+9	0	X	X	X	X	
6407-83.43	7.1	Postfl.	13	13	22	22	22	1	36	10+9	0	X	X	X	X	
5110-100.40	7.3	Postfl.	13	13	22	22	22	1	36	10+9	X	X	X	X	X	
6606-97.29	8.3	Postfl.	13	13	22	22	22	1	36	10+9	X	X	X	X	X	
Reared	11.0	Postfl.	13	13	24	23	23	1	37	10+9	X	X	X	X	X	
Reared	12.2	Juv.	13	13	22	22	22	1	36	10+9	X	X	X	X	X	
Reared	15.9	Juv.	13	13	22	22	22	1	36	10+10	X	X	X	X	X	
Reared	16.9	Juv.	13	13	22	22	22	1	36	10+9	X	X	X	X	X	
Santo Tomas	19.5	Juv.	13	13	23	23	23	1	37	10+9	X	X	X	X	X	
Bay, B.C.	26.5	Juv.	13	13	23	23	23	1	37	10+9	X	X	X	X	X	

¹Prefl. - preflexion; E fl. - early flexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.²Abbreviations in heading: n.pr. - neural process; h.pr. - haemal process; vert. - vertebrae; Sup. hyp. - Superior hypurals; Inf. hyp. - Inferior hypurals.³Asterisk indicates incomplete count.FIGURE 11.—Development of the caudal fin and supporting bones in *Pleuronichthys verticalis*. A. 5.3 mm NL; B. 6.9 mm NL; C. 8.3 mm SL. Ossified ural bones are shown in black; ossified elements of first preural vertebra are stippled. Ural bones include four hypurals, one epural, and the ural centrum.

the small upper superior hypural by 7.3 mm SL. Sixteen of the 19 caudal rays are supported by the four hypural bones, one by the epural and one each by the neural and haemal spines of the ultimate vertebra.

The vertebral column begins to ossify at about the same time rays begin forming in the caudal fin (Table 11). A 5.6-mm NL specimen which has 2+2 caudal rays has the first seven haemal processes of

main superior hypural and the two inferior hypurals are ossifying in specimens 6.9 mm NL and larger, the single epural by 7.0 mm SL, and

the caudal group of vertebrae forming. A slightly more advanced 5.5-mm NL specimen has 14 opposing neural and haemal processes of caudal vertebrae formed as well as the four anteriormost and last two precaudal neural processes. A neural or haemal process consists of two portions—a divided basal portion that forms the neural or haemal arch ending in the second portion as a terminal spine. On the 5.5-mm NL specimen, only the tips of the neural spines of the caudal group are ossified. Of the precaudal group, ossification first occurs in the arched portion of the anterior four neural processes and on the tips only of the last two precaudal neural spines. On a 5.8-mm NL specimen with the first 7 and last 4 precaudal neural processes and 17 pairs of neural and haemal processes in the caudal group ossifying, all of the neural processes except those of the 7 anterior precaudal vertebrae were ossifying initially from both ends, i.e., from the distal tips of the neural spines and from the basal portion of the neural arches, with ossification from both ends proceeding medially (Figure 12A). In a 6.1-mm NL specimen all 13 precaudal neural processes and 19 neural and haemal processes in the caudal group are ossified (Figure 12B). A 7.0-mm

NL late flexion specimen has all neural and haemal processes ossified except those on the terminal preural vertebra, but no centra are ossified. A 6.9-mm NL specimen, with all neural and haemal processes ossifying, has various stages of vertebral centra ossification with initial ossification of centra occurring below the bases of the neural and haemal arches and then filling in medially; only the two vertebral centra adjacent to the urostyle lack any ossification; the six vertebrae immediately forward of these have the best ossified centra. A 7.0-mm SL specimen has all centra ossified.

The bases of the dorsal and anal fins are present on larvae as small as 5.3 mm NL and rays begin to form by late flexion. Full complements of dorsal and anal fin rays are present on most postflexion specimens. Buds of the pelvic fins were first seen on a 6.1-mm NL specimen, and the complete count of six rays per fin is developed by 8.3 mm SL. Pectoral rays form only toward the end of the transformation stage after the left eye has nearly completed its migration to the right side.

Branchiostegal rays form progressively anteriorward during the period of caudal fin forma-

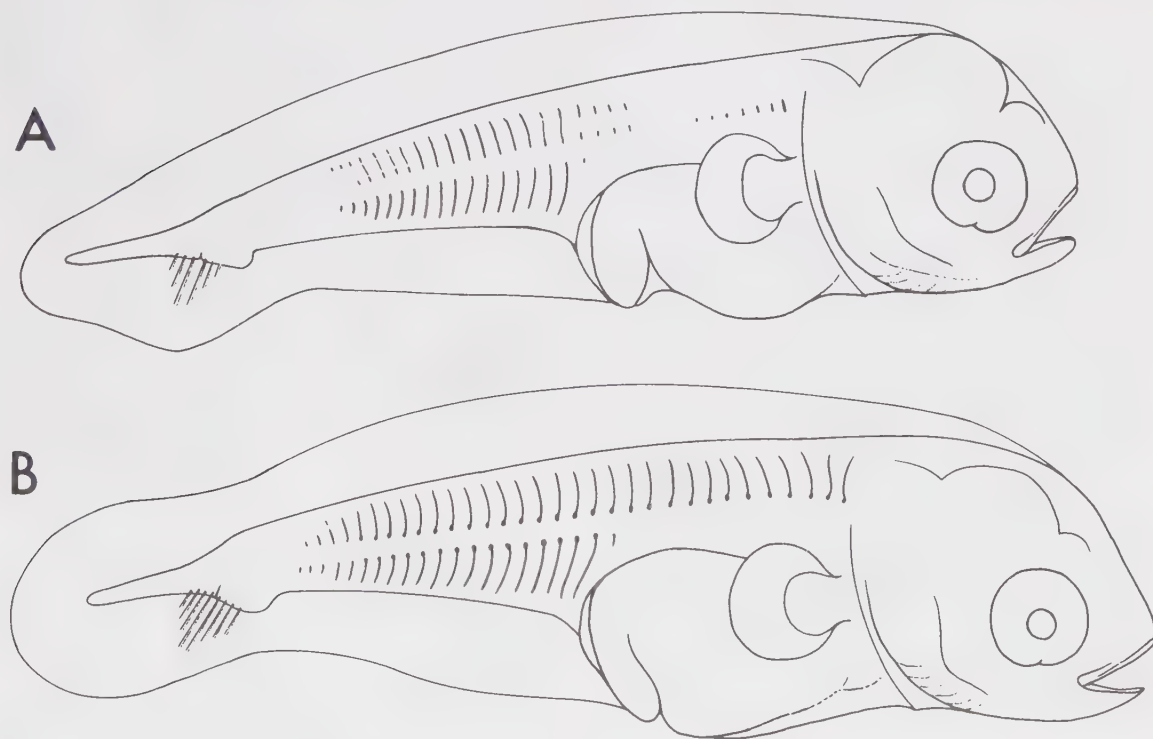


FIGURE 12.—Ossification pattern of the axial skeleton of *Pleuronichthys verticalis*: A. 5.8 mm; B. 6.1 mm.

tion between 5.6 and 6.9 mm NL, and the full count of seven rays per side is present on late flexion specimens. Gill rakers begin to develop by late flexion, but the full count is not obtained until the early juvenile stage. Few teeth form during the larval period. Only a single tooth is developed on the right side of the upper jaw in postflexion larvae, compared with 3-6 on the left side of this jaw. The disproportion is less marked in the lower jaw, with 3-5 teeth on the right side compared with 5-7 on the left side.

Distribution.—This species ranges from Point Reyes, Calif., south to Magdalena Bay, Baja California, with an isolated population at the northern end of the Gulf of California (Norman 1934; Fitch 1963). Eggs and larvae are common in our collections, particularly at inshore stations located over the continental shelf, with only an occasional specimen being taken more than 60 mi from the coast (Figure 13).

Pleuronichthys ocellatus Starks and
Thompson (Gulf turbot)
Figure 14

Literature.—Neither eggs nor larvae have been described previously.

Distinguishing characters.—This species may only be confused with *P. verticalis* or *H. guttulata* which cooccur with it in the upper Gulf of California. Larvae may be distinguished from *P. verticalis* by the lower total vertebral number of 34 or 35 and pigmentation differences. The larger size of larvae, lack of pterotic spines, and different pigment pattern separate it from *H. guttulata*. Meristics of the larvae and juveniles, given in Table 12, are distinctive for the species.

Pigmentation.—Only two postflexion larvae (6.6 mm SL and 7.0 mm SL) were available. Both specimens are heavily pigmented and somewhat resemble similar stages of *P. verticalis* larvae (Figure 14 vs. Figure 9D). However, smaller sized larvae of *P. ocellatus* are heavier in pigment than *P. verticalis* in regions of the head and dorsal and anal fin pterygiophores. Only the margin of the opercle, otic region, pectoral fin, and caudal peduncle remain unpigmented.

Morphology.—Larvae of *P. ocellatus* are intermediate in size between comparable stages of *P.*

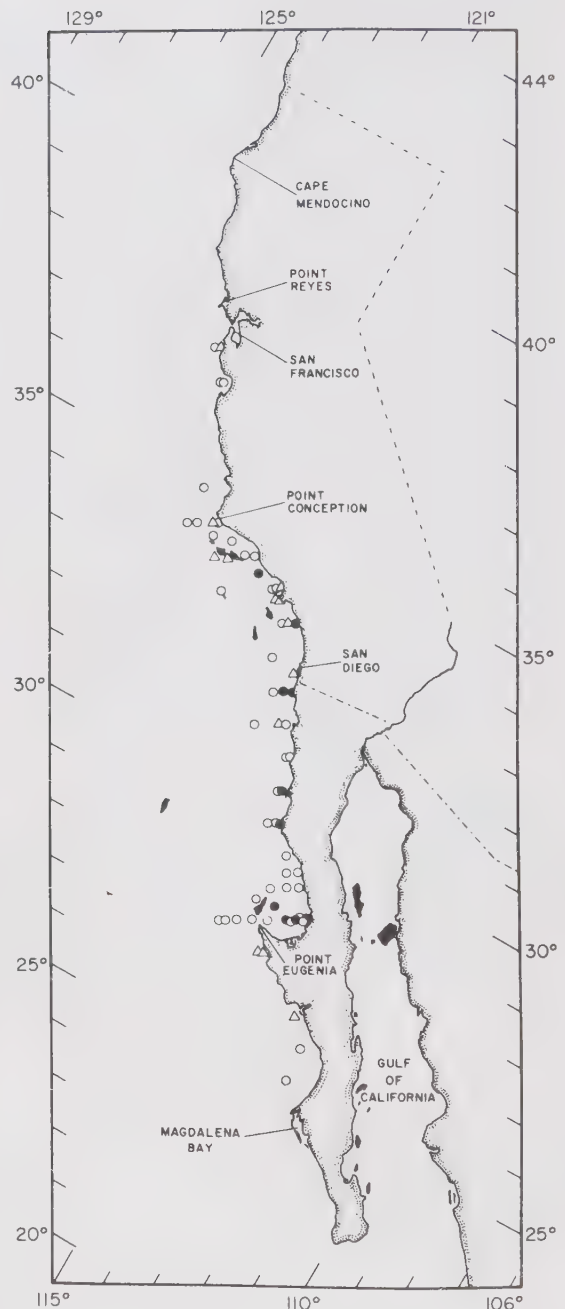
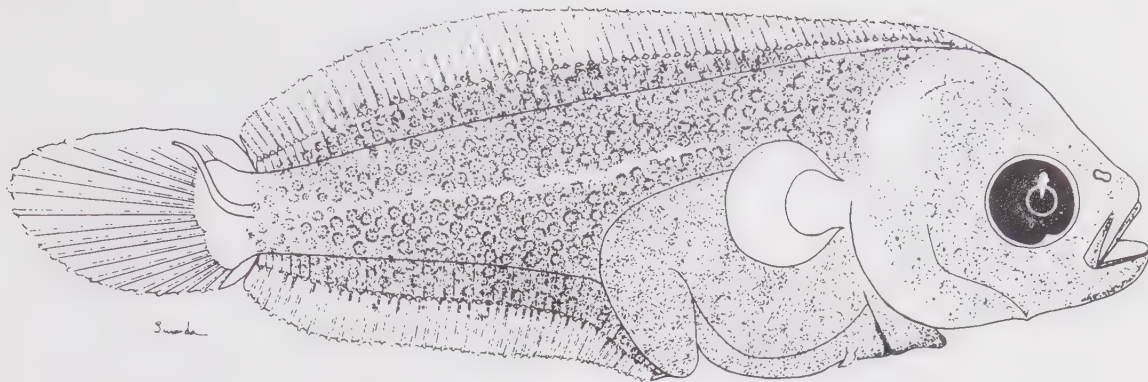


FIGURE 13.—Distribution of eggs and larvae of *Pleuronichthys verticalis* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

ritteri and *P. verticalis* (Table 13). It is the most slender-bodied species having the smallest body depth ratios in the postflexion larval stage within its genus (Table 5).

FIGURE 14.—*Pleuronichthys ocellatus* larva, 7.0 mm.TABLE 12.—Meristics of larvae and juveniles of *Pleuronichthys ocellatus*.

Station	Size (mm)	Stage ¹	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
5604-111.G.14	6.6 SL	Postfl.	65	49	19	ca. 4/4	LP ²				
5604-109.G.25	7.0	Postfl.	73	50	19	ca. 3/3	LP ²				
Upper Gulf of California	19.2	Juv.	64	46	19	6/6	10/11	12	22	34	X-ray
	22.0	Juv.	73	49	19	6/6	10/10	12	24	36	X-ray
	24.0	Juv.	67	48	19	6/6	—/11	12	22	34	X-ray
	24.5	Juv.	71	51	19	6/6	11/10	12	23	35	X-ray
	25.0	Juv.	70	50	19	6/6	11/10	12	22	34	X-ray
	25.5	Juv.	68	46	19	6/6	10/10	12	23	35	X-ray

¹Postfl. - postflexion; Juv. - juvenile.²LP refers to functional larval pectoral fins which have no ossified rays.TABLE 13.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys ocellatus*.

Station	Body length	Left eye ¹	Notochord ²	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base	Body depth at anus	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
5604-111.G.14	6.6 SL	Sym.	Flexed	3.2	2.0	0.30	0.54	0.56	2.2	2.2	0.50	0.40	1.9
5604-109.G.25	7.0	Sym.	Flexed	3.3	2.1	0.40	0.62	0.56	2.3	2.3	0.52	0.50	2.1
Upper Gulf of California	19.2	Over	Juv.	7.0	5.7	0.83	1.8	—	8.2	9.0	2.4	1.2	5.0
	22.0	Over	Juv.	7.0	6.2	0.91	1.9	—	9.4	9.8	2.8	1.4	5.2
	24.0	Over	Juv.	7.7	6.5	0.91	2.1	—	9.4	10.2	2.8	1.4	5.7
	24.5	Over	Juv.	7.4	6.8	1.1	2.3	—	10.5	11.0	3.2	1.5	5.5
	25.0	Over	Juv.	7.5	6.7	0.83	2.5	—	10.4	11.2	3.2	1.7	5.7
	25.5	Over	Juv.	8.5	6.8	0.91	2.3	—	10.7	11.7	3.1	1.8	6.0

¹Sym. - symmetrical.²Juv. - juvenile.

Distribution.—This species is restricted to the northern half of the Gulf of California (Norman 1934; Fitch 1963). Larvae were collected at two stations in the upper Gulf.

***Pleuronichthys ritteri* Starks and
Morris (spotted turbot)
Figures 15-17**

Literature.—The egg of *P. ritteri* was described by Orton and Limbaugh (1953) and illustrated by White (1977). Larvae of this species have not been described previously.

Distinguishing characters.—Larval stages of this

species may be confused with *P. verticalis* and *H. guttulata*. Characters of preflexion and flexion larvae which separate it from *P. verticalis* include the lack of triangular clusters of pigment on the finfold, less pigment on the tail with 8 or 9 unpigmented myomeres compared with 3-5 in *P. verticalis*, and a more robust body. Postflexion larvae are more heavily pigmented, particularly on the dorsal and anal fin pterygiophores, and are smaller than comparable stages of *P. verticalis*. Distinguishing characters for newly transformed and early juvenile stages have been discussed earlier under *P. verticalis*.

Characters for distinguishing yolk-sac larvae of *P. ritteri* from *H. guttulata* include the presence of

pigment on the finfolds of *P. ritteri*, a smaller oil globule (average 0.10 vs. 0.14 mm), lack of pigment on the oil globule, and presence of pigment ventrally near the tip of the notochord. Distinctive characters of preflexion and flexion larvae of *P. ritteri* include the lack of pterotic spines on the head which is more rounded than on preflexion *H. guttulata*, the lack of pigment from the top of the head posteriorly to the nape, a more robust head and trunk (compare Figure 15D with Figure 19D), and the presence of small pigment spots on the pectoral fin blade along its margin or base. Postflexion and early transforming specimens can be distinguished by a deeper and shorter caudal peduncle, a more robust body, and the origin of the dorsal fin on the future blind side of the head instead of on the medial line of the head as found in *H. guttulata*.

Pigmentation.—Yolk-sac larvae are heavily pigmented with the exception of the last 8 or 9 myomeres. Pigment is also scattered on the remnant of the yolk sac, on the dorsal and ventral finfolds, and ventrally on the tail near the tip of the notochord (Figure 15A). Except for the appearance of pigment along the margins of the pectoral fin blade, no significant changes in pigmentation occur in early preflexion larvae of ca. 3.0 mm NL (Figure 15B).

By 4.0 mm NL, pigment found earlier along the top of the head posterior to the nape is lost, leaving an unpigmented streak which persists until flexion of the notochord is complete at 5.5 mm NL (Figures 15C, D; 16A, B). Ventral pigment is similarly lost on the abdominal region, resulting in an unpigmented lower abdomen in late preflexion and flexion specimens. Marginal pectoral fin pigment present on larvae to about 3.3 mm NL, changes to small, discrete spots on the fin membrane along its base. These melanophores persist through postflexion larvae until the pectoral fin differentiates into a small, rayed fin by ca. 10.0 mm SL (Figures 16C, 17).

Pigment on the tail extends posteriad the same distance in flexion larvae as in preflexion larvae, but in postflexion larvae the tail pigment fills in posteriorly to the terminal dorsal and anal fin rays. In later postflexion and transformation stages, the head, trunk, and tail, except the caudal peduncle, are completely covered with pigment which extends over the dorsal and anal fin pterygiophores (Figures 16C, 17).

At 10.0 mm SL, a dark circular blotch of pigment develops on the middle section of the body, with a heavy band of pigment at the posterior extreme of body pigment. Several triangular patches are clustered on the dorsal and anal fin rays above the pterygiophores. The caudal peduncle area remains unpigmented (Figure 17).

Morphology.—Larvae of *P. ritteri* are the smallest among species of *Pleuronichthys* in comparable stages of development. Our smallest specimen has a large yolk sac and is 2.1 mm NL (Figure 15A). The oil globule is positioned posteriorly in the yolk mass and measures 0.11 mm in diameter. The left eye begins to migrate at about 6.0 mm SL and migration of the eye is completed before 10.0 mm SL (Table 14). The smallest available juvenile was 12.7 mm SL.

The gut develops as in other *Pleuronichthys* but coiling begins earlier, at about 3.0 mm NL, and the terminal section of the gut is in a vertical position in most specimens >4.0 mm NL.

The head is relatively larger in preflexion larvae of *P. ritteri* than in the other species (Table 5). Relative head length increases throughout the larval period, then is moderately reduced at transformation. Mean relative snout length increases in *P. ritteri* larvae undergoing notochord flexion and decreases during subsequent stages, but in other species of *Pleuronichthys* it decreases during all major phases of larval development. Relative eye size is largest in preflexion larvae, becomes reduced in later larval stages, and increases at transformation.

The early larvae of *P. ritteri* are the deepest bodied species of *Pleuronichthys*. Mean relative body depth measured at the base of the pectoral fin is greater during preflexion and flexion stages of the notochord than in any other species. In postflexion larvae, however, mean relative body depth is markedly less than in *P. decurrens* and about equal to that in *P. coenosus* and *P. verticalis* (Table 5).

Fin and axial skeleton formation.—Early caudal formation involving thickening in the hypural area of the developing caudal fin occurs on larvae 4.3–5.1 mm NL (Table 15). Caudal rays are forming on larvae as small as 4.5 mm NL, with a simultaneous initiation of flexion of the notochord. Specimens between 4.5 and 5.6 mm NL undergo notochord flexion. Our smallest specimen with a fully flexed notochord is 5.3 mm SL. The full

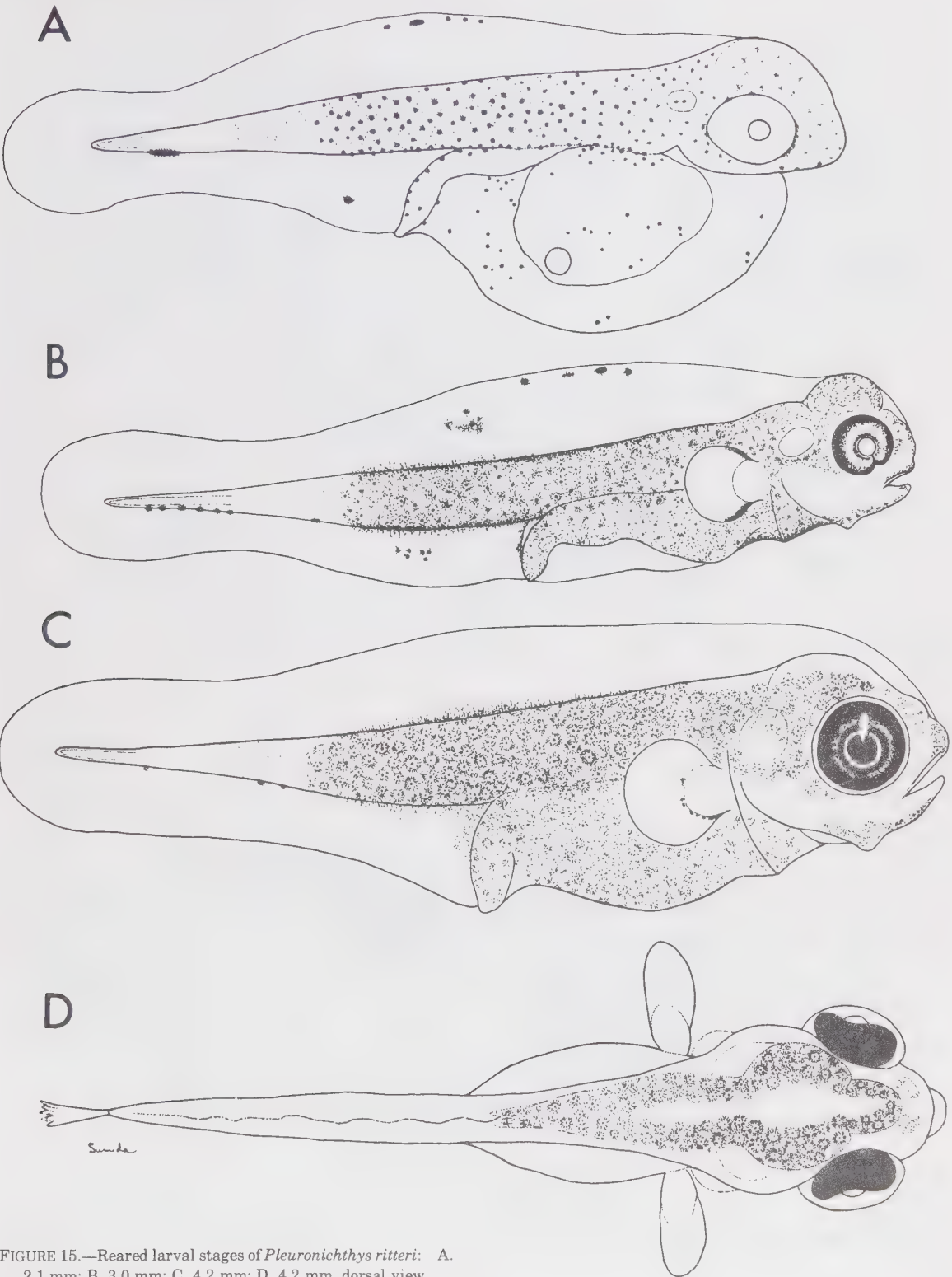


FIGURE 15.—Reared larval stages of *Pleuronichthys ritteri*: A. 2.1 mm; B. 3.0 mm; C. 4.2 mm; D. 4.2 mm, dorsal view.

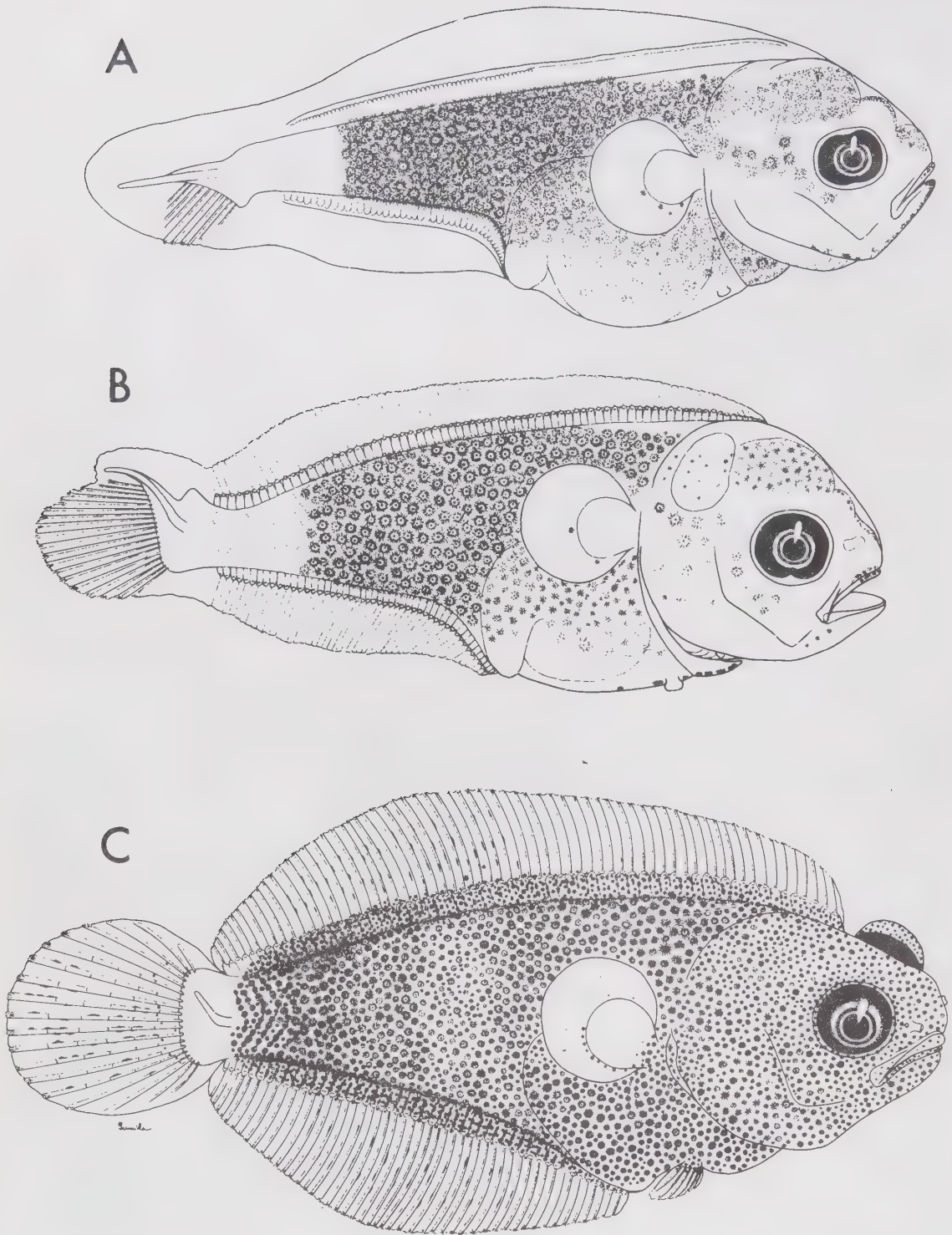
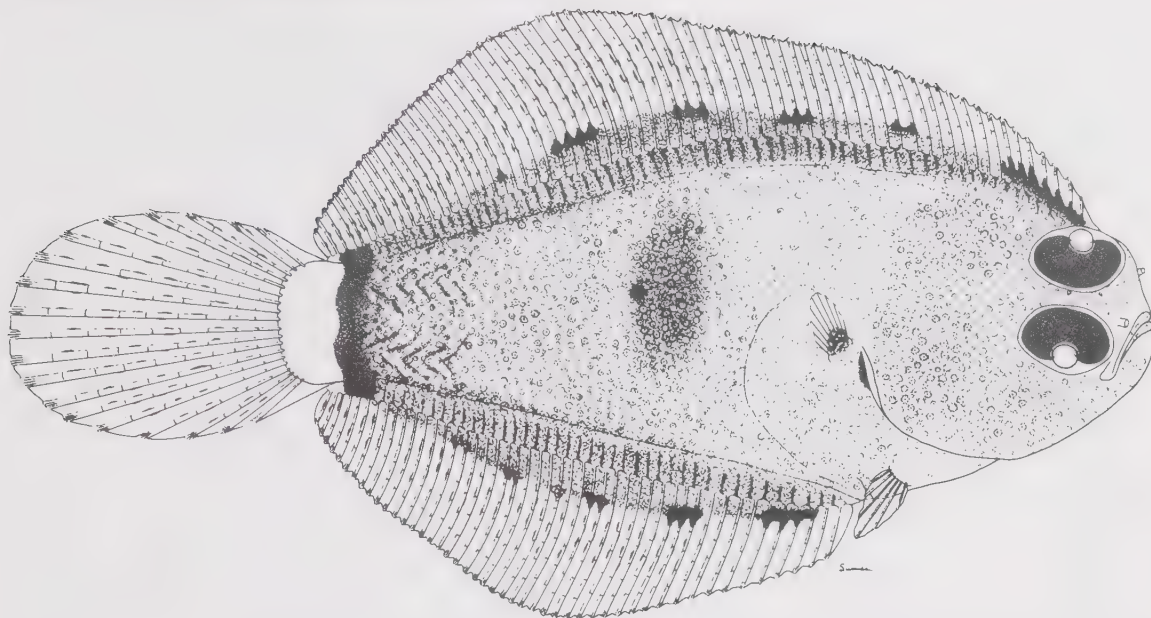


FIGURE 16.—Larval stages of *Pleuronichthys ritteri*: A. 5.6 mm; B. 5.5 mm; C. 6.4 mm.

FIGURE 17.—Transforming specimen of *Pleuronichthys ritteri*, 10.0 mm.TABLE 14.—Morphometrics, in millimeters, of larvae and juveniles of *Pleuronichthys ritteri*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye ¹	Notochord ²	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base ³	Body depth at anus ³	Caudal peduncle depth	Caudal peduncle to length	Snout to origin pelvic fin
Off La Jolla, Calif.	2.1 NL	Sym.	Str.	1.2	0.50	0.10	0.24	0.20	0.20	0.38	—	—	—
	3.0	Sym.	Str.	1.4	0.60	0.12	0.26	0.22	0.42	0.42	—	—	—
7412-123.36	3.3	Sym.	Str.	1.6	0.80	0.14	0.28	0.24	0.78	0.58	—	—	—
Off La Jolla	4.2	Sym.	Str.	2.2	1.0	0.18	0.40	0.32	0.96	0.86	—	—	—
5709-117.26	4.3	Sym.	Str.	2.1	1.1	0.20	0.40	0.36	1.2	1.2*	—	—	—
7207-123.36	4.4	Sym.	Str.	2.1	1.1	0.24	0.34	0.32	1.0	0.9	—	—	—
6204-120.25	5.0	Sym.	Str.	2.2	1.2	0.20	0.38	0.38	1.2	1.1*	—	—	—
5708-120.25	5.1	Sym.	Str.	2.5	1.4	0.24	0.46	0.40	1.8*	1.7*	—	—	1.3
6507-120.35	4.5	Sym.	E fl.	2.3	1.4	0.32	0.44	0.42	1.6*	1.6*	—	—	1.2
5506-120.40	4.8	Sym.	E fl.	2.3	1.4	0.28	0.40	0.38	1.5*	1.7*	—	—	1.4
5510-117.26	5.5	Sym.	Midfl.	2.7	1.2	0.34	0.52	0.48	2.0*	1.9*	—	—	1.6
7501-120.25	5.6	Sym.	Midfl.	2.7	1.5	0.26	0.46	0.40	1.8*	1.5*	—	—	1.4
5112-120.35	5.3 SL	Sym.	Flexed	2.7	1.7	0.30	0.52	0.52	2.2*	2.2*	0.50	0.36	1.4
5802-137.23	6.0	Migr.	Flexed	2.9	2.0	0.32	0.60	0.54	2.4*	2.7*	0.66	0.30	1.8
Off La Jolla	6.4	Migr.	Flexed	2.6	2.2	0.40	0.64	0.60	2.5*	2.7*	0.76	0.38	2.0
Sebastian Viscaino Bay, B.C.	7.5	A. over	Flexed	3.0	2.6	0.40	0.80	0.64	2.9*	3.0*	1.0	0.48	2.7
7501-120.22.4	8.5	A. over	Flexed	2.8	2.7	0.40	0.86	?	3.6*	3.6*	1.1	0.44	2.3
Off La Jolla	10.0	Over	Flexed	3.1	3.1	0.48	1.0	0.80	4.2*	4.2*	1.4	0.60	2.6
Reared	12.7	Over	Juv.	4.2	3.8	0.36	1.4	1.0	5.1*	5.4*	1.4	0.76	3.4
Reared	15.0	Over	Juv.	4.5	4.2	0.48	1.6	1.2	5.9*	6.1*	1.8	1.0	3.9
Reared	16.7	Over	Juv.	5.2	4.7	0.48	1.8	1.4	6.2*	6.4*	2.0	1.1	4.2
Off San Juanico, B.C.	23.0	Over	Juv.	7.2	6.8	0.83	2.2	?	9.7*	9.7*	2.6	1.2	5.8

¹Sym. - symmetrical; Migr. - migrating; A. over - About over.²Str. - straight; E fl. - early flexion; Midfl. - midflexion; Juv. - juvenile.³Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

caudal count of 19 rays was observed on a 6.0-mm SL postflexion specimen.

Dorsal and anal fin bases are forming in the finfold on larvae 4.3 mm NL, and the full comple-

ment of rays develops by 6.0 mm SL. Pelvic fin buds are evident during early caudal formation but rays are first observed on a 6.0-mm specimen. Pectoral rays were fully formed on a 10.0-mm

TABLE 15.—Meristics of larvae and juveniles of *Pleuronichthys ritteri*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage ¹	Fin rays					Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic	Pectoral right/left	Precaudal	Caudal	Total	
Off La Jolla, Calif.	2.1 NL	Yolk-sac	0	0	0	0	LP ²				
	3.0	Prefl.	0	0	0	0	LP ²				
7412-123.36	3.3	Prefl.	0	0	0	0	LP ²				
Off La Jolla	4.2	Prefl.	0	0	0	0	LP ²				
5709-117.26	4.3	Prefl.	Forming	Forming	Forming	0	LP ²				
7207-23.36	4.4	Prefl.	Forming	Forming	Forming	0	LP ²				
6204-120.25	5.0	Prefl.	Forming	Forming	Forming	0	LP ²				
5708-120.25	5.1	Prefl.	Forming	Forming	Forming	Bud	LP ²				
6507-120.35	4.5	E fl.	Forming	Forming	ca. 6	Bud	LP ²				
5506-120.40	4.8	E fl.	Forming	Forming	ca. 4	Bud	LP ²				
5510-117.26	5.5	Midfl.	Forming	Forming	ca. 8	Bud	LP ²				
7501-120.25	5.6	Midfl.	Forming	Forming	ca. 8	Bud	LP ²				
5112-120.35	5.3 SL	Postfl.	ca. 60	ca. 45	16	Bud	LP ²				
5802-137.23	6.0	Postfl.	72	49	19	6/6	LP ²				
Off La Jolla	6.4	Postfl.	65	45	19	6/6	LP ²				
Sebastian Viscaino Bay, B.C.	7.5	Postfl.	70	48	19	6/6	LP ²				
7501-120.22.4	8.5	Postfl.	69	51	19	6/6	LP ²				
Off La Jolla	10.0	Postfl.	68	47	19	6/6	9/9	12	23	35	X-ray
Reared	12.7	Juv.	69	47	19	6/6	10/11	12	23	35	X-ray
Reared	15.0	Juv.	64	44	19	6/6	10/11	12	23	35	X-ray
Reared	16.7	Juv.	65	44	19	6/6	11/11	12	22	34	X-ray
Off San Juanico, B.C.	23.0	Juv.	68	49	Damaged	6/6	9/9	12	23	35	X-ray

¹Prefl. - preflexion; E fl. - early flexion; Midfl. - midflexion; Postfl. - postflexion; Juv. - juvenile.²LP refers to functional larval pectoral fins which have no ossified rays.

larva. A radiograph of this specimen showed 12 precaudal and 23 caudal vertebrae, the typical count for this species.

Distribution.—This species ranges from Morro Bay, Calif., to Magdalena Bay, Baja California (Fitch 1963; Miller and Lea 1972; Fierstine et al. 1973). Our egg and larval material, which was collected between southern California and Magdalena Bay, Baja California, shows a markedly coastal, inshore distribution for *P. ritteri*, with a majority of collections made over or near the continental shelf (Figure 18).

Hypsopsetta guttulata Girard
(diamond turbot)
Figures 19-22

Literature.—Orton and Limbaugh (1953) and Orton (1953) briefly described the eggs of *H. guttulata*. Eldridge (1975) described and illustrated larvae of this species, and noted the average size of its egg and oil globule. Although the larval series is quite well described in Eldridge (1975) (except for the omission of the pterotic spine on the head), we are including information about distinguishing characters, pigmentation, etc. to facilitate identification.

Distinguishing characters.—Larvae of *H. guttulata* are distinguishable from species of *Pleuronichthys*, except for *P. ritteri*, by their lower total vertebral number, by attaining comparable stages of development at smaller sizes, and by the presence of a pterotic spine on each side of the head in yolk-sac larvae to midflexion larvae. In the genus *Pleuronichthys*, only *P. decurrens* develops pterotic spines. (See Distinguishing characters for *P. decurrens*.)

The only species with which larval *H. guttulata* may be confused is *P. ritteri* because of its relatively small size and somewhat similar pigment pattern. (See Distinguishing characters for separating larvae of the two species discussed under *P. ritteri*.)

Pigmentation.—Yolk-sac larvae are heavily pigmented on the head, trunk, and for a short distance on the tail, with the posteriormost 9 or 10 myomeres remaining unpigmented (Figure 19A). Pigment spots are scattered over the ventral and posterior surfaces of the yolk sac and oil globule, and over the terminus of the gut.

Preflexion larvae show little change in pigment pattern. One or two melanophores develop on the pectoral fin base. The isthmus has a line of pigment spots, and the entire abdominal area is covered with pigment (Figure 19B).

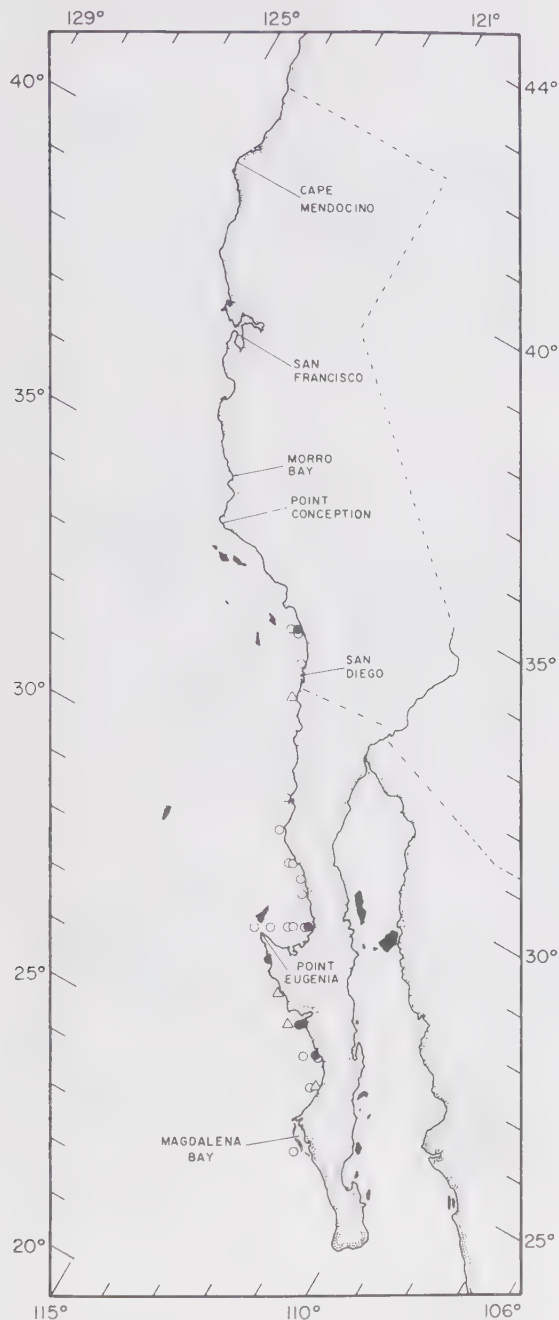


FIGURE 18.—Distribution of eggs and larvae of *Pleuronichthys ritteri* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

At the initiation of dorsal and anal fin formation, the tail pigment spreads out dorsally and ventrally onto the finfold, resulting in conspicuous

dark mounds of pigment opposing each other in the area between the body and the dorsal and anal fin bases (Figure 19C). The tops of the head, nape, and shoulder area are pigmented in contrast to *P. ritteri*, which has an unpigmented streak dorsally (Figure 19D). Flexion, postflexion, and early transforming specimens maintain the earlier pigment pattern and the only obvious change is a slight posteriad extension of trunk pigment, leaving 5 or 6 unpigmented myomeres posteriorly compared with 9 or 10 in earlier stages (Figure 20). The base of the pectoral fin acquires more pigment spots in postflexion larvae, and pigment on the head similarly increases in density (Figure 20B).

Preserved small juveniles are brownish-black with numerous small, dark spots scattered over the body and pterygiophores, giving them a mottled appearance (Figure 21).

Morphology.—Our smallest yolk-sac larva is 2.2 mm NL and has a posteriorly positioned oil globule 0.14 mm in diameter (Figure 19A). The left eye is beginning to migrate in a specimen 4.4 mm SL and is complete in a 7.3-mm SL larva (Table 16). The smallest available juvenile was 11.2 mm SL.

A major distinguishing feature of *Hypsopsetta* larvae is the presence of a pterotic spine on each side of the head. The spines are present on the smallest yolk-sac larva and are prominent in most preflexion larvae. The spines begin to regress on late preflexion larvae, and are totally regressed in late flexion specimens. In *P. decurrens* the spines are well developed throughout the larval period and begin to regress late in the postflexion stage.

Although mean relative body depth of *H. guttulata* larvae increases with development, it is slightly less in postflexion specimens than in any species of *Pleuronichthys*, except *P. ocellatus* (Table 5). In newly transformed juveniles, however, relative body depth is greater than in any species of *Pleuronichthys*. As a juvenile, *H. guttulata* assumes a diamond-shaped body form.

Relative body width is useful to separate *Hypsopsetta* larvae from those of *P. ritteri*. As shown in Figures 15D and 19D, larvae of *Hypsopsetta* have narrower bodies.

Fin formation.—The caudal fin forms on larvae between 4.0 and 5.2 mm NL and is complete on some specimens as small as 4.4 mm (Table 17). The dorsal and anal fins form simultaneously with the

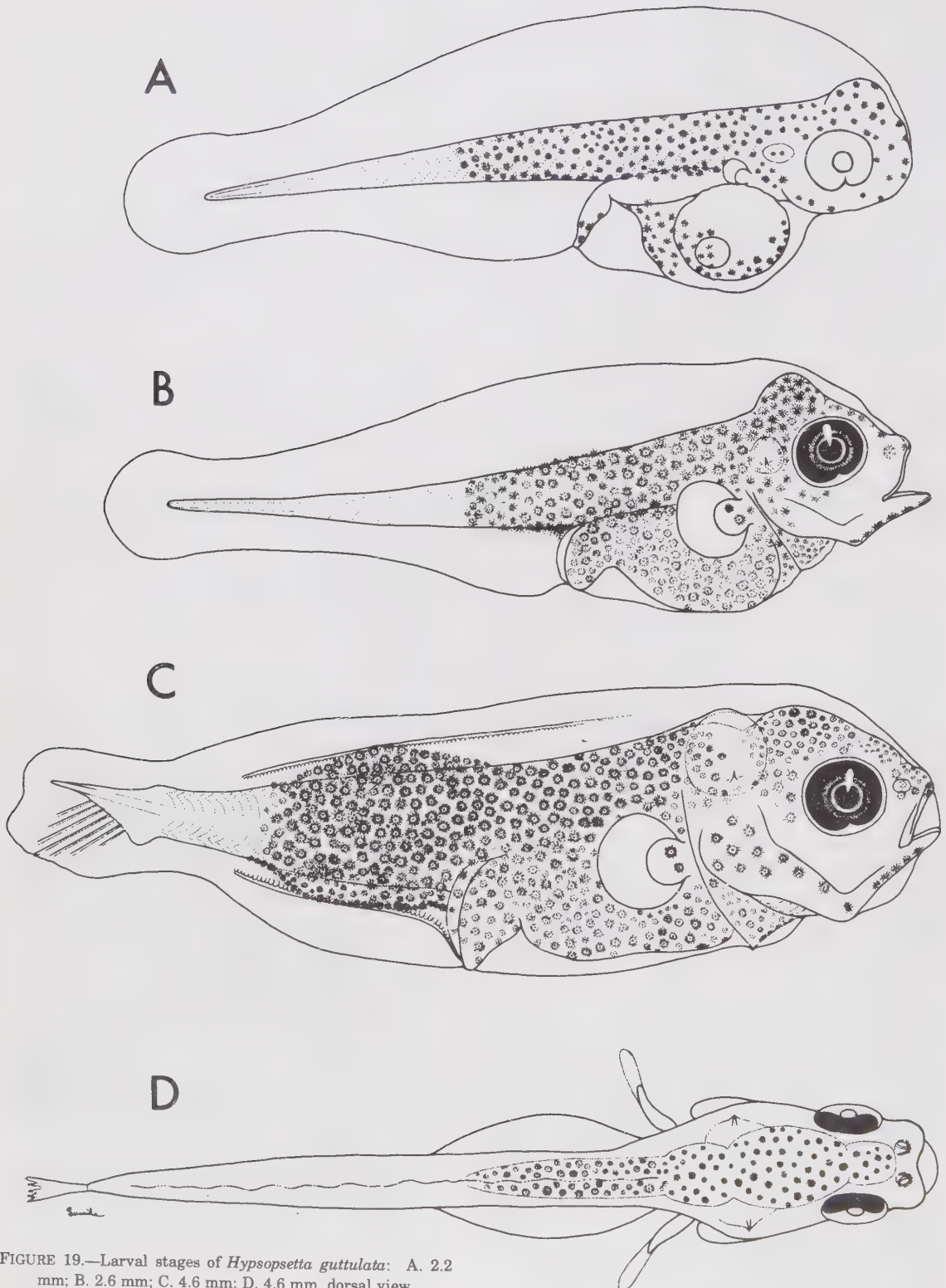


FIGURE 19.—Larval stages of *Hypsopsetta guttulata*: A. 2.2 mm; B. 2.6 mm; C. 4.6 mm; D. 4.6 mm, dorsal view.

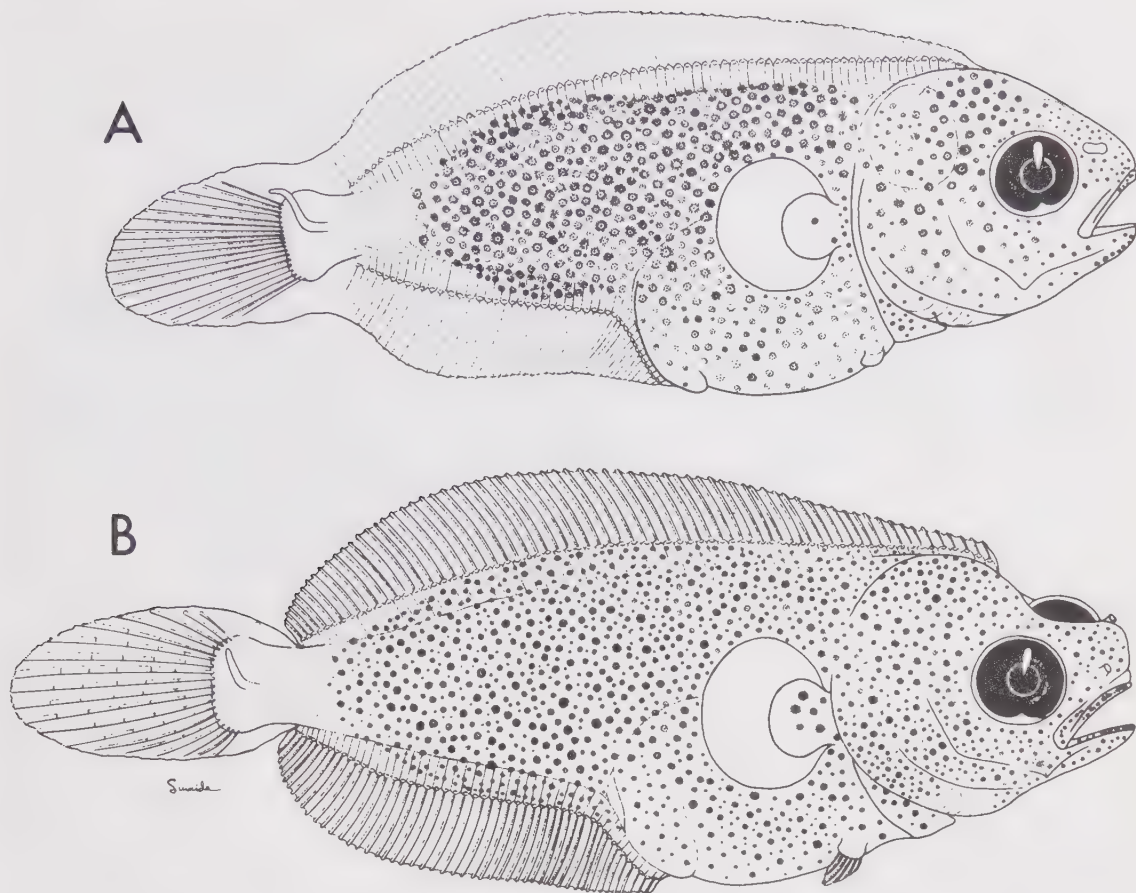


FIGURE 20.—Larval stages of *Hypsopsetta guttulata*: A. 5.9 mm; B. 6.6 mm.

caudal and are complete, or nearly so, on all post-flexion specimens (4.4–8.8 mm SL). Pelvic fins are late in forming compared with their developmental pattern in *Pleuronichthys* larvae. Pelvic buds can be observed only after notochord flexion has been completed, and rays are first evident on the 6.6-mm SL specimen.

Distribution.—*Hypsopsetta guttulata* ranges from Cape Mendocino, Calif., to Magdalena Bay, Baja California, with an isolated population in the upper Gulf of California (Norman 1934; Fitch 1963). Egg and larval material examined by us was collected in bays along the coast, or at CalCOFI stations located over the continental shelf, a pattern of distribution similar to the habitat of *P. ritteri* (Figure 22).

Hippoglossina stomata Eigenmann
and Eigenmann (bigmouth sole)
Figure 23

Literature.—There is no published account of eggs and larvae of this species. However, Leonard (1971) described a larval series of *H. oblonga* from the western North Atlantic. Earlier, Agassiz and Whitman (1885) and Miller and Marak (1962) described the eggs and early-stage larvae of *H. oblonga*. Miller and Marak reported the egg size range as 0.91–1.12 mm (average 1.04 mm) with an oil globule diameter of ca. 0.17 mm. The larval size at hatching was 2.7–3.2 mm.

Distinguishing characters.—Preflexion larvae of *H. stomata* may be confused with early larvae of *P.*



FIGURE 21.—Early juvenile of *Hypsopsetta guttulata*, 13.2 mm.

coenosus and *P. verticalis* due to similarities in size and pigmentation of the larvae, and the presence of pigment on the finfold dorsally and ventrally, posterior to the anus. Characters of *H. stomata* larvae which distinguish them from preflexion *P. coenosus* larvae include the presence of a pigment bar through the eye, heavy pigment on both sides of the pectoral fin base and a sprinkling of pigment on the pectoral blade, a more slender, elongate body, and a significantly smaller patch of dorsal finfold pigment. The same characters help to distinguish *H. stomata* from *P. verticalis*, except for the finfold pigmentation. *Pleuronichthys verticalis* has small, triangular-shaped pigment patches whereas *H. stomata* has a small rounded pigment cluster on the dorsal finfold and a broad patch on the ventral finfold. Larvae of *P. verticalis* are also smaller than *H. stomata* at similar developmental stages.

Larvae in the flexion stage and larger are readily separable from *Pleuronichthys* by the preopercular spines and development of several elongated dorsal rays in the anteriormost part of the dorsal fin. These do not develop on larval *Pleuronichthys* or *Hypsopsetta*.

Pigmentation.—Yolk-sac larvae (ca. 3.7 mm) are heavily pigmented on the trunk and tail except for the posteriormost part of the tail which is pigmented with several small spots dorsally and ventrally (Figure 23A). The upper head and abdominal region have scattered pigment, with a more concentrated bar of pigment on each side of the eye. Both sides of the pectoral fin base are conspicuously pigmented. Finfold pigment consists of a small, rounded patch at the edge of the dorsal finfold, and a broad patch on the ventral finfold, both situated posterior to the anus near the midpoint between the anus and tip of the tail (Figure 23A).

Preflexion larvae, 4.1-7.0 mm NL, undergo little change in pigmentation except to augment pigment in areas of the pectoral fin, abdominal region, and top of the head (Figure 23B).

On larvae forming the dorsal and anal fins, the dorsal finfold pigment spreads to include the area between the fin rudiments and body margin, and the ventral finfold pigment spreads both anteriorly and posteriorly (Figure 23C). Pigment on the pectoral fin base intensifies and also extends out onto the fin blade.

TABLE 16.—Morphometrics, in millimeters, of larvae and juveniles of *Hypsopsetta guttulata*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye ¹	Notochord ²	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base ³	Body depth at anus ³	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
San Diego Bay	2.2 NL	Sym.	Str.	1.1	0.38	0.08	0.17	0.13	0.18	0.28	—	—	—
King Harbor, Calif.	2.3	Sym.	Str.	1.1	0.46	0.12	0.20	0.17	0.18	0.34	—	—	—
7501-120.25	2.8	Sym.	Str.	1.4	0.68	0.12	0.26	0.22	0.62	0.52	—	—	—
7501-120.29	3.3	Sym.	Str.	1.7	0.82	0.20	0.30	0.24	0.82	0.72	—	—	—
San Diego Bay	3.6	Sym.	Str.	1.8	0.84	0.16	0.32	0.28	0.78	0.66	—	—	—
San Diego Bay	4.0	Sym.	Str.	2.0	0.88	0.20	0.36	0.30	0.88	0.84	—	—	—
7412-127.32.6	4.4	Sym.	Str.	2.2	0.90	0.20	0.37	0.32	1.0	0.92	—	—	—
7412-127.32.6	4.6	Sym.	E fl.	2.3	1.2	0.24	0.38	0.32	1.1	1.0	—	—	—
7501-120.22.4	4.9	Sym.	E fl.	2.4	1.3	0.22	0.40	0.36	1.2	1.1	—	—	—
7501-120.29	5.1	Sym.	E fl.	2.5	1.2	0.22	0.40	0.36	1.1	1.1	—	—	—
King Harbor	5.2	Sym.	L fl.	2.4	1.4	0.28	0.44	0.42	1.2	1.2	—	—	—
L.A. Harbor, Calif.	4.4 SL	Migr.	Flexed	2.2	1.6	0.30	0.48	0.42	1.8*	1.9*	0.40	0.40	1.4
La Jolla, Calif.	4.8	Migr.	Flexed	2.2	1.5	0.30	0.48	0.40	1.6*	1.7*	0.40	0.36	1.4
San Diego Bay	5.4	Migr.	Flexed	2.3	1.8	0.34	0.52	0.40	1.8*	1.9*	0.42	0.42	1.6
7501-120.22.7	5.9	Sym.	Flexed	3.1	1.8	0.32	0.50	0.46	2.0*	2.2*	0.44	0.48	1.9
7501-120.24	6.6	Migr.	Flexed	3.2	2.1	0.40	0.62	0.52	2.3*	2.4*	0.50	0.60	2.0
Reared	7.3	Over	Flexed	2.9	2.5	0.40	0.90	0.70	3.3*	3.5*	0.76	0.64	2.1
Reared	7.9	Over	Flexed	2.9	2.7	0.44	0.92	0.68	3.6*	3.8*	0.86	0.70	2.1
Reared	8.8	Over	Flexed	3.6	3.0	0.48	1.0	0.76	4.1*	4.2*	0.96	0.68	2.6
Reared	11.2	Over	Juv.	4.2	3.7	0.50	1.4	1.1	5.7*	6.0*	1.4	1.0	3.3
Richardson Bay, Calif.	12.9	Over	Juv.	4.5	4.3	0.52	1.2	0.92	7.0*	7.0*	1.5	1.0	3.6
	13.2	Over	Juv.	4.8	4.3	0.75	1.3	1.1	6.7*	7.1*	1.4	1.0	3.6
	14.0	Over	Juv.	5.0	4.7	0.75	1.4	1.2	7.5*	7.7*	1.6	1.2	3.8
	14.5	Over	Juv.	5.2	4.8	0.72	1.4	1.0	7.7*	7.9*	1.8	0.88	4.1
	18.4	Over	Juv.	6.4	5.8	0.80	1.7	1.4	10.0*	10.5*	2.1	1.4	5.1

¹Sym. - symmetrical; Migr. - migrating.²Str. - straight; E fl. - early flexion; L fl. - late flexion; Juv. - juvenile.³Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.TABLE 17.—Meristics of larvae and juveniles of *Hypsopsetta guttulata*. (Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage ¹	Fin rays				Pectoral right/left	Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic		Precaudal	Caudal	Total	
7501-120.25	2.8 NL	Prefl.	0	0	0	0	LP ²				
7501-120.29	3.3	Prefl.	0	0	0	0	LP ²				
San Diego Bay	3.6	Prefl.	0	0	0	0	LP ²				
San Diego Bay	4.0	Prefl.	Forming	Forming	Forming	0	LP ²				
7412-127.32.6	4.4	Prefl.	Forming	Forming	6	0	LP ²				

7412-127.32.6	4.5	E fl.	Forming	Forming	8	0	LP ²				
7501-120.22.4	4.9	E fl.	Forming	Forming	6	0	LP ²				
7501-120.29	5.1	E fl.	Forming	Forming	4	0	LP ²				
King Harbor, Calif.	5.2	L fl.	ca. 50	ca. 35	15	0	LP ²				

L.A. Harbor, Calif.	4.4 SL	Postfl.	67	47	19	Bud	LP ²				
Off La Jolla, Calif.	4.8	Postfl.	66	49	19	Bud	LP ²				
San Diego Bay	5.4	Postfl.	73	45	19	Bud	LP ²				
7501-120.22.7	5.9	Postfl.	73	46	19	Bud	LP ²				
7501-120.24	6.6	Postfl.	69	50	19	6/6	LP ²				
Reared	7.3	Postfl.	68	47	19	6/6	11/11	11	23	34	X-ray
Reared	7.9	Postfl.	67	51	20	6/6	12/12	12	23	35	X-ray
Reared	8.8	Postfl.	72	50	19	6/6	13/13	12	23	35	X-ray
Reared	11.2	Juv.	73	48	19	4/6	12/12	12	22	34	X-ray
Richardson Bay, Calif.	12.9	Juv.	66	48	19	6/6	12/11	12	23	35	X-ray
	13.2	Juv.	74	53	19	6/6	11/11	12	23	35	X-ray
	14.0	Juv.	78	55	19	6/6	11/11	12	23	35	X-ray
	14.5	Juv.	71	51	19	6/6	12/12	12	23	35	X-ray
	18.4	Juv.	68	51	19	6/6	11/12	12	23	35	X-ray

¹Prefl. - preflexion; E fl. - early flexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.²LP refers to functional larval pectoral fins which have no ossified rays.

Postflexion and early transforming specimens are less heavily pigmented than earlier stage larvae, with a noticeable diminution of pigment on the dorsal area of the head and body (Figure 23D).

Morphology.—Larvae of *H. stomata* are closest to *P. coenosus* in size at hatching, notochord flexion, and transformation (Table 18). A specimen 3.7 mm NL has a moderate amount of yolk remaining.

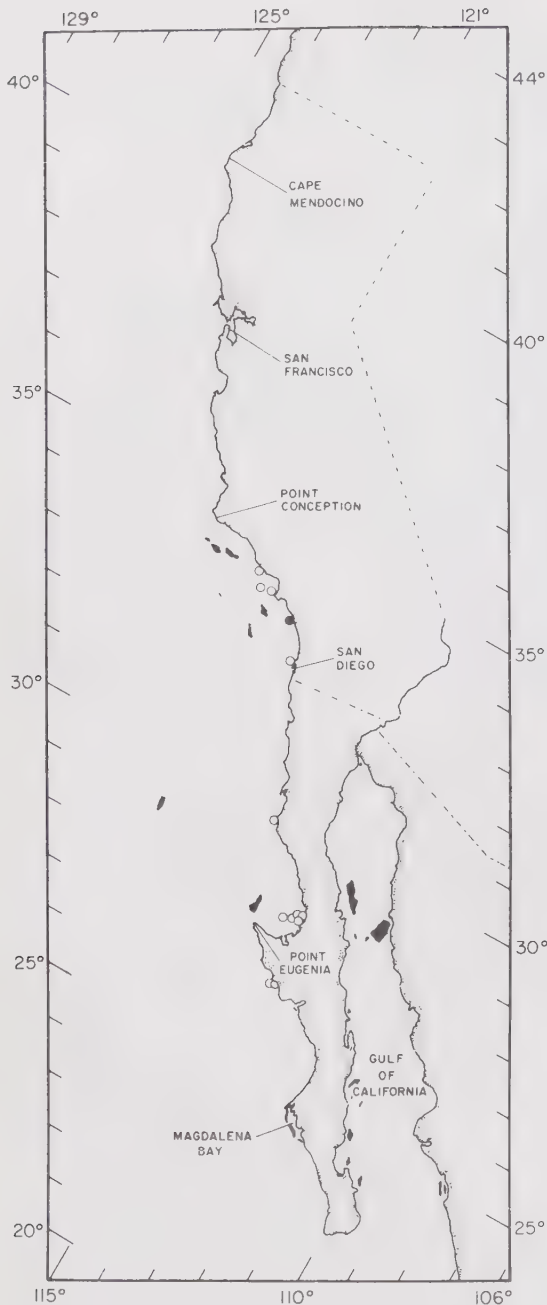


FIGURE 22.—Distribution of eggs and larvae of *Hypsopsetta guttulata* examined in this study. (Open circles represent larvae, closed circles eggs and larvae.)

The right eye is beginning to migrate in a specimen 9.1 mm SL and transformation is almost complete at 11.7 mm SL.

In early preflexion larvae of *Hippoglossina*, the gut is shaped like that in *Pleuronichthys* larvae; however, coiling begins at about 4.5 mm NL and the gut assumes a more compact shape than in *Pleuronichthys*. This is reflected in the relatively shorter snout-anus length. Mean relative snout-anus length remains at about 40% of the body length throughout the larval period, in contrast to *Pleuronichthys* larvae in which there is a gradual decrease in relative gut length during larval development (Table 5). In juveniles, however, there is a decrease in snout-anus length to about 33% of body length, a value comparable with that in *Pleuronichthys* juveniles.

The head is similar in size and shape to that in *Pleuronichthys*. Relative head length increases gradually during larval development. The same is true for relative snout length and is thus opposite to the condition in *Pleuronichthys*; however, it decreases somewhat in juveniles. Relative eye width undergoes a moderate diminution during larval development as in *Pleuronichthys*, but increases moderately in juveniles.

Small preopercular spines develop on larvae from ca. 5.5 mm NL, become most conspicuous on flexion stage larvae, and undergo resorption during transformation from 9.5 mm SL. This spination is distinctive of *H. stomata* when compared with *Pleuronichthys* and *Hypsopsetta*.

Larvae of *Hippoglossina* have a slender appearance compared with some of the deeper bodied species of *Pleuronichthys*. Body depth at the anus is comparatively small in preflexion larvae and remains so in flexion and postflexion larvae and early juveniles (Table 5).

As in *Hypsopsetta*, the caudal peduncle is longer and more slender than in *Pleuronichthys*, except for *P. ocellatus* postflexion larvae.

Fin formation.—Larvae of *Hippoglossina stomata* are comparable with those of *P. coenosus* with regard to size at which the caudal fin develops. Caudal fin formation occurs between 6.2 and 8.8 mm NL (Table 19). Although about six caudal rays are formed on a 7.0-mm NL specimen with a straight notochord, all other specimens with caudal rays have the notochord flexing. The smallest, fully flexed specimen is 7.1 mm SL. Postflexion specimens <9.0 mm SL lack the full complement of 18½ caudal rays. The ural bones supporting the caudal rays are made up of two superior and two inferior hypurals; there is no epural. The lack of an epural bone is a specific

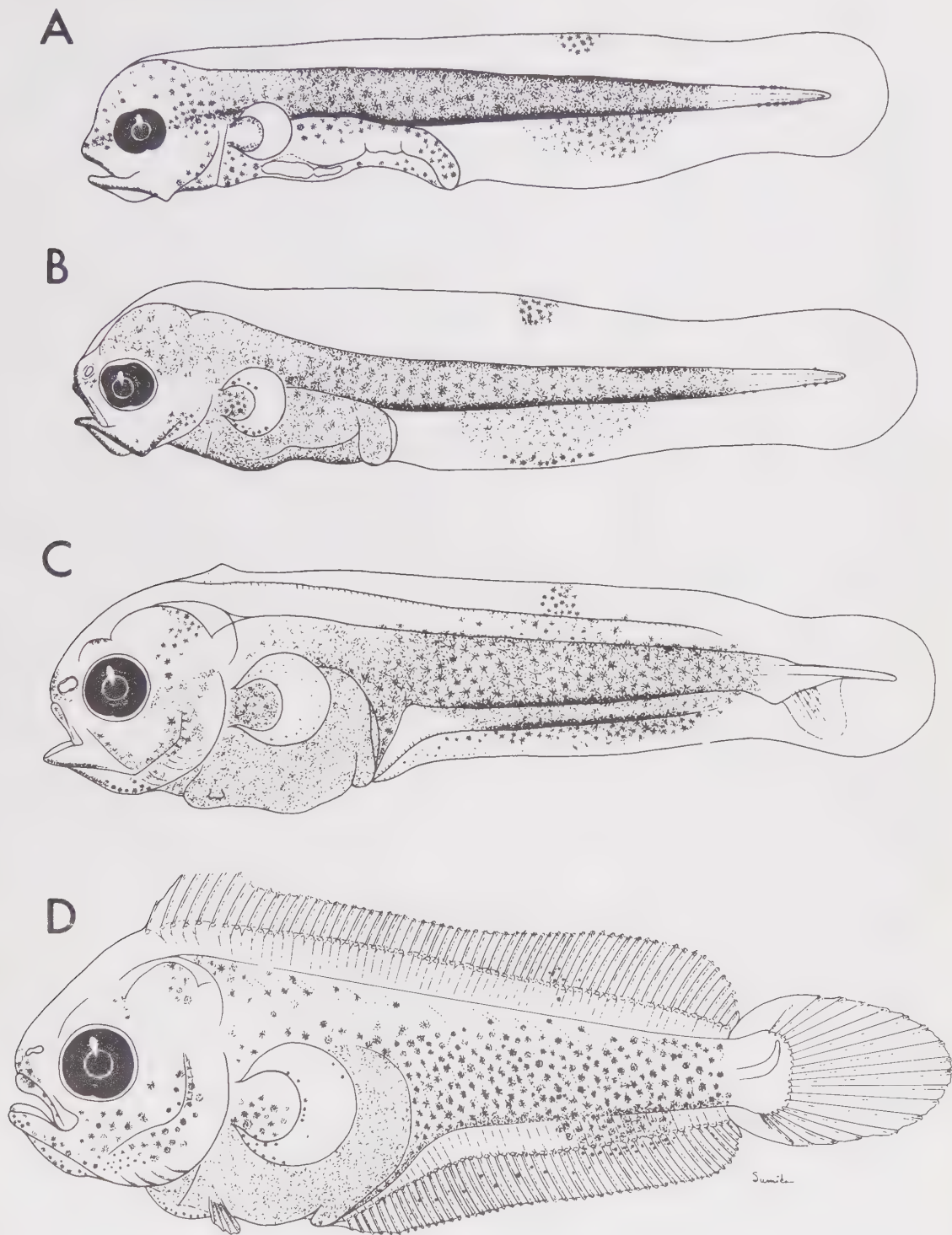


FIGURE 23.—Larval stages of *Hippoglossina stomata*: A. 3.8 mm; B. 4.8 mm; C. 8.3 mm; D. 8.6 mm.

TABLE 18.—Morphometrics, in millimeters, of larvae of *Hippoglossina stomata*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Body length	Left eye ¹	Notochord ²	Snout to anus	Head length	Snout length	Eye width	Eye height	Body depth at P base ³	Body depth at anus ³	Caudal peduncle depth	Caudal peduncle length	Snout to origin pelvic fin
7201-117.35	3.7 NL	Sym.	Str.	1.4	0.64	0.10	0.28	0.21	0.50	0.40	—	—	—
7412-103.29	4.1	Sym.	Str.	1.8	0.72	0.07	0.24	0.24	0.48	0.36	—	—	—
7412-88.5.31	4.8	Sym.	Str.	2.0	1.0	0.24	0.36	0.28	0.96	0.68	—	—	—
5801-117.35	5.2	Sym.	Str.	2.2	1.2	0.24	0.48	0.36	1.2	0.82	—	—	—
6310-93.28	6.2	Sym.	Str.	2.2	1.3	0.26	0.42	0.36	1.2	0.92	—	—	—
6605-123.37	6.4	Sym.	Str.	2.2	1.3	0.24	0.44	0.36	1.4*	1.0	—	—	—
5910-117.30	6.2	Sym.	Str.	2.8	1.6	0.30	0.54	0.42	2.1*	1.3	—	—	—
6706-110.50	7.0	Sym.	Str.	2.8	1.8	0.32	0.50	0.42	2.1*	1.8*	—	—	—
5708-118.5.35	6.6	Sym.	E fl.	2.7	1.7	0.40	0.54	0.54	2.1*	1.7*	—	—	1.5
5706-127.34	7.5	Sym.	E fl.	3.0	2.0	0.36	0.66	0.70	2.2*	1.8*	—	—	1.8
6912-83.60	8.3	Sym.	E fl.	3.2	1.8	0.42	0.60	0.66	2.4*	2.0*	—	—	2.0
5807-130.30	7.6	Sym.	Midfl.	2.9	1.9	0.38	0.64	0.58	2.2*	2.0*	—	—	1.8
5709-110.30	7.9	Sym.	Midfl.	2.9	1.9	0.42	0.60	0.52	2.2*	2.0*	—	—	1.7
6706-123.37	8.8	Sym.	Midfl.	3.4	2.3	0.44	0.68	0.60	2.8*	2.4*	—	—	2.4
5706-123.37	7.6	Sym.	L fl.	3.1	2.1	0.46	0.66	0.64	2.5*	2.3*	—	—	1.8
6706-123.36	8.5	Sym.	L fl.	3.4	2.3	0.44	0.70	0.66	2.8*	2.6*	—	—	2.3
6608-120.30	7.1 SL	Sym.	Flexed	3.1	2.2	0.46	0.76	0.78	2.6*	2.4*	0.66	0.62	2.1
5708-115.35	8.0	Sym.	Flexed	3.3	2.4	0.64	0.72	0.68	2.9*	2.7*	0.62	0.70	2.0
6706-123.37	9.0	Sym.	Flexed	3.9	2.7	0.52	0.84	0.84	3.4*	3.0*	0.70	0.82	2.7
6410-83.43	9.4	Sym.	Flexed	3.7	2.7	0.56	0.84	0.84	3.6*	3.8*	0.80	0.84	2.3
5701-120.35	9.1	Migr.	Flexed	3.8	3.1	0.72	1.0	0.96	3.7*	4.1*	0.92	0.68	2.7
5709-110.33	9.9	Migr.	Flexed	4.0	3.2	0.80	0.90	0.86	4.1*	4.3*	0.90	0.76	2.6
6706-123.36	10.5	Migr.	Flexed	4.1	3.5	0.80	1.1	0.94	3.8*	3.9*	0.98	0.88	3.0
5507-130.30	11.7	Migr.	Flexed	4.2	3.7	0.96	1.0	0.88	4.4*	4.5*	1.2	0.90	3.5
Asuncion Bay,	35.8	Over	Juv.	12.4	12.2	2.3	4.3	—	13.4*	13.0*	3.2	2.9	10.5
B.C.	38.2	Over	Juv.	12.2	13.5	2.7	4.2	—	14.2*	13.7*	3.8	3.4	11.4

¹Sym. - symmetrical; Migr. - migrating.²Str. - straight; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Juv. - juvenile.³Asterisk indicates inclusion of dorsal fin pterygiophores in body depth measurement.

TABLE 19.—Meristics of larvae and juveniles of *Hippoglossina stomata*.
(Specimens between dashed lines are undergoing notochord flexion.)

Station	Size (mm)	Stage ¹	Fin rays				Pectoral right/left	Vertebrae			Source of count
			Dorsal	Anal	Caudal	Pelvic		Precaudal	Caudal	Total	
7201-117.35	3.7 NL	Prefl.	0	0	0	0	LP ²				
7412-103.29	4.1	Prefl.	0	0	0	0	LP ²				
7412-88.5.31	4.8	Prefl.	0	0	0	0	LP ²				
5801-117.35	5.2	Prefl.	0	0	0	0	LP ²				
6310-93.28	6.2	Prefl.	0	0	0	0	LP ²				
6605-123.37	6.4	Prefl.	Anterior swelling	0	0	0	LP ²				
5910-117.30	6.2	Prefl.	Forming	0	Forming	0	LP ²				
6706-110.50	7.0	Prefl.	Forming	Forming	ca. 6	0	LP ²				
5708-118.5.35	6.6	E fl.	Forming	Forming	ca. 6	Bud	LP ²				
5706-127.34	7.5	E fl.	Forming	Forming	ca. 10	Bud	LP ²				
6912-83.60	8.3	E fl.	Ant. 4	Forming	ca. 10	Bud	LP ²				
5807-130.30	7.6	Midfl.	ca. 15	ca. 15	12	Bud	LP ²				
5709-110.30	7.9	Midfl.	ca. 55	ca. 45	12	Bud	LP ²				
6706-123.37	8.8	Midfl.	ca. 62	ca. 50	16	Bud	LP ²				
5706-123.36	7.6	L fl.	ca. 63	ca. 45	14	Bud	LP ²				
6706-123.36	8.5	L fl.	ca. 68	ca. 50	14	Bud	LP ²				
6608-120.30	7.1 SL	Postfl.	ca. 66	ca. 51	16	ca. 5/5	LP ²				
5708-115.35	8.0	Postfl.	63	50	ca. 18	6/6	LP ²				
6706-123.37	9.0	Postfl.	68	53	18½	5/5	LP ²				
6410-83.43	9.4	Postfl.	68	54	ca. 18	6/6	LP ²				
5701-120.35	9.1	Postfl.	67	53	18½	6/6	LP ²				
5709-110.33	9.9	Postfl.	65	50	18½	6/6	LP ²				
6706-123.36	10.5	Postfl.	66	53	18½	6/6	LP ²				
5507-130.30	11.7	Postfl.	64	50	18½	6/6	LP ²				
Asuncion Bay,	35.8	Juv.	67	52	18½	6/6	10/10	11	27	38	X-ray
B.C.	38.2	Juv.	65	50	17½	6/6	10/10	11	27	38	X-ray

¹Prefl. - preflexion; E fl. - early flexion; Midfl. - midflexion; L fl. - late flexion; Postfl. - postflexion; Juv. - juvenile.²LP refers to functional larval pectoral fins which have no ossified rays.

character in *H. stomata* because other species of *Hippoglossina* possess this bone.

The dorsal fin of *H. stomata* develops quite differently than in *Pleuronichthys*. An anterior group of about five dorsal rays is the first to form in *H. stomata*; these become more elongated than the other rays. The anlage of these is evident on a 6.4-mm NL preflexion specimen and four rays are formed on a 9.3-mm NL early flexion larva. A similar pattern of early forming dorsal fin rays is found in the closely related genera *Paralichthys* (Okiyama 1967; Smith and Fahay 1970; Ahlstrom and Moser 1975) and *Pseudorhombus* (Devi 1969). Although the anterior dorsal rays form early, the pelvic fins do not develop elongated rays, such as in the bothid genera *Syacium* (Aboussouan 1968) and *Cyclopsetta* (Gutherz 1970). The dorsal fin rays differentiate posteriorly but most rays form simultaneously and the full complement is developed on a late flexion specimen. The base of the anal fin is evident during early caudal formation, rays are forming on midflexion specimens, and the total number is formed on a late flexion specimen. Pelvic fin buds are evident on early flexion specimens, but rays can be distinguished only on post-flexion larvae.

Distribution.—This species ranges from Monterey Bay, Calif., to the Gulf of California, including Guadalupe Island (Miller and Lea 1972). Larvae occurred over a wide band of inshore and offshore stations (Figure 24). The southern limit of *H. stomata* overlaps the northern range of *H. tetraphthalmus* which has different fin counts (Ginsburg 1952). To date, larvae of *H. tetraphthalmus* are not known.

SUMMARY

We used a combination of larval morphology, meristics, and pigmentation to distinguish seven known eastern North Pacific species of flatfishes with heavily pigmented larvae. Table 20 summarizes many pertinent characters for identifying eggs and larvae of these species. Information is given for three characters of eggs: size, ornamentation of the chorion, and presence or absence of an oil globule.

In most instances, the size of a newly hatched larva is directly related to the size of the egg from which it hatched, and such is the case with *Pleuronichthys*. *Pleuronichthys decurrens*, with the largest egg, has the largest larva, with a suc-

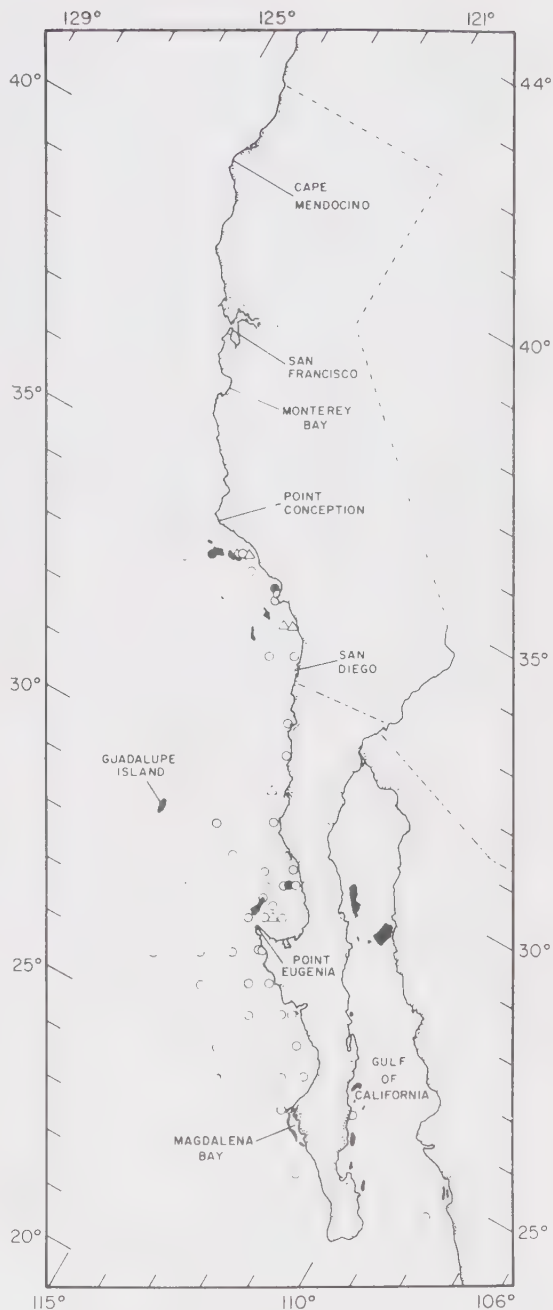


FIGURE 24.—Distribution of eggs and larvae of *Hippoglossina stomata* examined in this study. (Triangles represent eggs, open circles larvae, and closed circles eggs and larvae.)

cessive decrease in larval size of the other species corresponding to their smaller sized eggs. This also applies to the yolk-sac larvae of *Hypsopsetta guttulata* and *Hippoglossina stomata*. *Pleuron-*

ichthys decurrens, with the largest yolk-sac larva, is correspondingly large at caudal fin formation (notochord flexion) and at transformation, whereas *Hypsopsetta guttulata*, with the smallest egg, is correspondingly smallest at all stages of larval development with the exception of some overlap with larvae of *P. ritteri*.

A larval character that is particularly useful in separating preflexion larvae of *H. guttulata* from those of *P. ritteri* is the presence of a pterotic spine on each side of the head of *H. guttulata*. The only species of *Pleuronichthys* with a pterotic spine is *P. decurrens*.

For relating a larval series to its juveniles and adults, and thus substantiating identification of the series, meristic counts, particularly of the pre-caudal and caudal groups of vertebrae, are indispensable. One can seldom rely on one meristic character alone, but must use a combination of all available counts.

The distribution of pigment, which changes with growth, provides good characters for discriminating among larvae of the several species. It is particularly useful with preflexion larvae, and for this reason we emphasize pigment for this stage in Table 20.

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TABLE 20.—Summary of egg and larval characters useful in identifying flatfishes with heavily pigmented larvae.

Characters	<i>Pleuronichthys decurrens</i>	<i>P. coenosus</i>	<i>P. verticalis</i>	<i>P. ocellatus</i>	<i>P. ritteri</i>	<i>Hypopselta guttulata</i>	<i>Hippoglossina stomata</i>
Eggs							
Diameter	1.84-2.08	1.20-1.56	1.00-1.16	No data	0.94-1.08	0.78-0.89	1.22-1.38
Chorion	Polygonal sculpturing	Polygonal	Polygonal	No data	Polygonal	Smooth	Smooth
Oil globule	0	0	0		1 (0.10 mm)	1 (0.13 mm)	1 (0.23 mm)
Larval morphology:							
Size of available yolk-sac larvae (mm NL)	4.9 (5.54-Budd 1940)	3.9 (3.88-Budd 1940)	2.4 (3.16-Budd 1940)	No data	2.1	2.2-2.3 (1.7-2.1-Eldridge 1975)	3.7
Size range of preflexion larvae	4.9-9.8	3.7-8.5	2.4-5.8	No data	2.1-5.1	2.2-4.4	3.7-7.0
Size range at caudal fin formation (mm NL)	7.8-11.0	6.2-8.5	5.0-7.2	No data <6.6	4.3-5.6	4.0-5.2	6.2-8.8
Size range during transformation							
Pterotic spines (mm SL)	10.5-29.4	8.2-17.0	7.3-12.2	No data	6.0-12.7	4.4-11.2	9.1-11.7
Elongated anterior dorsal rays	1 on each side	0	0	0	0	1 on each side	0
Meristics							
Precaudal vertebrae	0	0	0	0	0	0	ca. 5
Caudal vertebrae	14-15 (14)	12-13 (13)	13	12-13 (12)	12-13 (12)	11-12 (12)	11
Caudal rays	24-26 (25) 18-20 (19)	24-26 (24-25) 19-21 (19)	22-25 (23) 19	22-24 (22-23) 18-19 (19)	22-24 (23) 19-20 (19)	22-24 (23) 19-20 (19)	26-28 (27) 17½-18½ (18½)
Pigmentation							
Finfold of early larvae	Entirely pigmented except for extreme posterior portion of tail	Opposing clusters approx. midway on tail region	Triangular cluster behind anus ventrally; dorsal cluster slightly forward of ventral cluster; persist through notochordal flexion	No data	Few scattered melanophores on distal margins near anus; these do not persist after long preservation. Often with expansion of melanophores along both margins of body posterior to anus	Opposing pigment extending from body posterior of the anus	Small rounded patch dorsally and broad patch ventrally from middle part of tail
Top of head to shoulder region in early larvae	Present	Present	Absent	No data	Absent	Present	Present but sparse
Unpigmented posterior tail region	Extreme tip of notochord only in very early larvae	Tip of notochord followed by narrow posterior band of caudal peduncle in later stages	Last 3 to 5 myomeres through early notochordal flexion, followed by unpigmented caudal peduncle (shorter than in <i>P. ritteri</i>)	Caudal peduncle in late larvae	Last 7 or 8 myomeres through notochordal flexion; entire caudal peduncle unpigmented where dorsal & anal fins terminate in transforming sizes	Last 9 to 10 myomeres prior to notochordal flexion; shortening to 5 or 6 myomeres after flexion	Tip of tail
Pectoral fin base or fin membrane prior to caudal fin formation	Few melanophores scattered on fin base	None	None	No data	Small melanophores along proximal margin of fin membrane	Two to three melanophores on fin base, particularly at symphysis	Dense pigment on fin base, sparse on fin membrane

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RECENT SIGHTINGS OF THE BLUE WHALE,
BALENOPTERA MUSCULUS, IN
THE NORTHEASTERN TROPICAL PACIFIC

The blue whale, *Balenoptera musculus*, in the North Pacific, migrates to the Gulf of Alaska and Aleutians in the summer for feeding (Nishiwaki 1966). It is believed to migrate to tropical waters in winter for calving, but sightings of blue whales in lower latitudes are rare (Tomilin 1957). In mid-July 1928, Cruikshank reported seeing "... several blue whales ..." at lat. 11°32'N and long. 91°58'W (Kellogg 1929). A Peruvian fishery reported taking 247 blue whales between December 1925 and March 1926 (Ingebrigtsen 1929). Potentially these were from a North Pacific stock, since the Southern Hemisphere blue whale is most numerous in the Antarctic at this time. Volkov and Moroz (1977) noted an abundance of baleen

whales between lat. 7° and 10°N. Although individual species of baleen whales were not enumerated by Volkov and Moroz, two sightings of blue whales were made on 29 March 1975 and are presented here (Table 1, *Vnushitelnyi* cruise).

Typically blue whales are seen along the Baja California coast in October while migrating southward, and subsequently reappear off Baja California in large numbers in March-June on their northward migration (Rice 1974). The whereabouts of the North Pacific blue whales during the winter months is completely unknown, but this is probably due to the lack of sighting effort. For instance, Japanese whale scouting has been carried out systematically since 1965, but their effort has been restricted to the Pacific waters north of lat. 20°N (Wada 1977).

Two theories have evolved regarding the wintering grounds of the blue whale. Wheeler (1946), suggested that blue whales winter within a limited area of the subtropics. He maintained that whales congregate in large groups in areas not frequented by vessels. A second theory maintains that wintering blue whales disperse between the feeding grounds and the tropics (Harmer 1931; Mackintosh 1942). Presented in this note is a 3-yr record of blue whales sighted in the northeastern tropical Pacific. Reference is made to migration, whale groupings, behavior, and to the oceanographic features of the sighting area. These recent sightings were made by trained observers aboard vessels involved with the National Marine Fisheries Service Tuna/Porpoise Research Pro-

gram. Sighting information from other experienced observers has also been contributed.

Shipboard identification of rorquals is difficult and this problem was compounded by the fact that most of the sightings mentioned in this paper were incidental to ship's activities. However, the blue whale is easily discerned from other rorquals by the recognition of the following combination of characteristics:

1. Mottled blue-grey coloration. All other rorquals are uniformly steel grey on the dorsal surface.
2. A small dorsal fin of varying shapes located in the posterior third of the body. The dorsal fin of the sei, fin, and brydes whales is larger, falcate shape, and placed farther anterior than the blue whale dorsal fin.
3. A U-shaped rostrum. The rostrum shape of other balenopterids is more pointed.
4. Tall, dense, disperse blows. Generally, the blow of the sei and brydes whales is low and dissipated, while the fin whale has a tall conical-shaped blow.

A total of 11 cruises are discussed in this report, covering the period from January to May for 1971, 1975, 1976, and 1977.¹ The area of effort and sightings of blue whales are reported in Figure 1. The

¹No blue whale sightings were made in 1977, although two cruises have been included in Figure 1 to complement survey effort.

TABLE 1.—Annotated list of blue whale sightings by National Marine Fisheries Service observers in the northeastern tropical Pacific, January-May 1971-76.

Date	Lat., Long.	No. of whales	Observations	Cruise/Observer
8 Jan. 1971	07°54'N, 095°52'W	1		<i>Nautilus</i> /Leatherwood
23 Jan. 1975	01°30'N, 083°04'W	1	Dove for 7 min	<i>Pan Pacific</i> /Friedrichsen
3 Feb. 1975	07°29'N, 093°48'W	cow and calf	3 dives, 5.57 min/dive; length: cow 27 m, calf 8-10 m	<i>Aquarius</i> /Wade
4 Feb. 1975	07°48'N, 097°40'W	1	Surfaced in middle of tuna school	<i>Finesterre</i> /Walker
7 Feb. 1975	07°45'N, 098°21'W	1	5 dives, 10.11 min/dive	<i>Aquarius</i> /Wade
7 Feb. 1975	07°47'N, 098°24'W	1	2 dives, 8.19 min/dive	<i>Aquarius</i> /Wade
7 Feb. 1975	07°52'N, 098°47'W	2	Small unidentified whale, 10 m, with visible blow, swimming with a large blue whale	<i>Aquarius</i> /Wade
7 Feb. 1975	07°47'N, 099°00'W	1	3 dives, 11.39 min/dive; exposed tail fluke on all dives	<i>Aquarius</i> /Wade
9 Feb. 1975	08°50'N, 096°04'W	4-6	Paired groups, length estimate: 27 m	<i>Pan Pacific</i> /Friedrichsen
10 Feb. 1975	08°33'N, 096°47'W	1		<i>Pan Pacific</i> /Friedrichsen
15 Feb. 1975	08°36'N, 096°29'W	1		<i>Pan Pacific</i> /Friedrichsen
17 Feb. 1975	08°58'N, 096°54'W	8-10	Mostly pairs dispersed over several square miles; all headed northeast	<i>Pan Pacific</i> /Friedrichsen
17 Feb. 1975	08°53'N, 096°36'W	1		<i>Pan Pacific</i> /Friedrichsen
29 Mar. 1975	08°55'N, 093°34'W	10-13		<i>Vnushitelnyi</i> /Rice
29 Mar. 1975	09°07'N, 093°55'W	6-7		<i>Vnushitelnyi</i> /Rice
13 Feb. 1976	09°44'N, 092°25'W	2		<i>Cromwell</i> /Friedrichsen et al
13 Feb. 1976	09°44'N, 092°31'W	1	Length estimate: 23 m	<i>Cromwell</i> /Friedrichsen et al
13 Feb. 1976	09°44'N, 092°35'W	4-5	Whales dispersed over 4-5 mi ²	<i>Cromwell</i> /Friedrichsen et al
13 Feb. 1976	09°44'N, 092°52'W	1	Exposed tail flukes prior to sounding	<i>Cromwell</i> /Friedrichsen et al
28 May 1976	10°31'N, 092°45'W	1	Length estimate: 20 m	<i>Martinac</i> /Friedrichsen

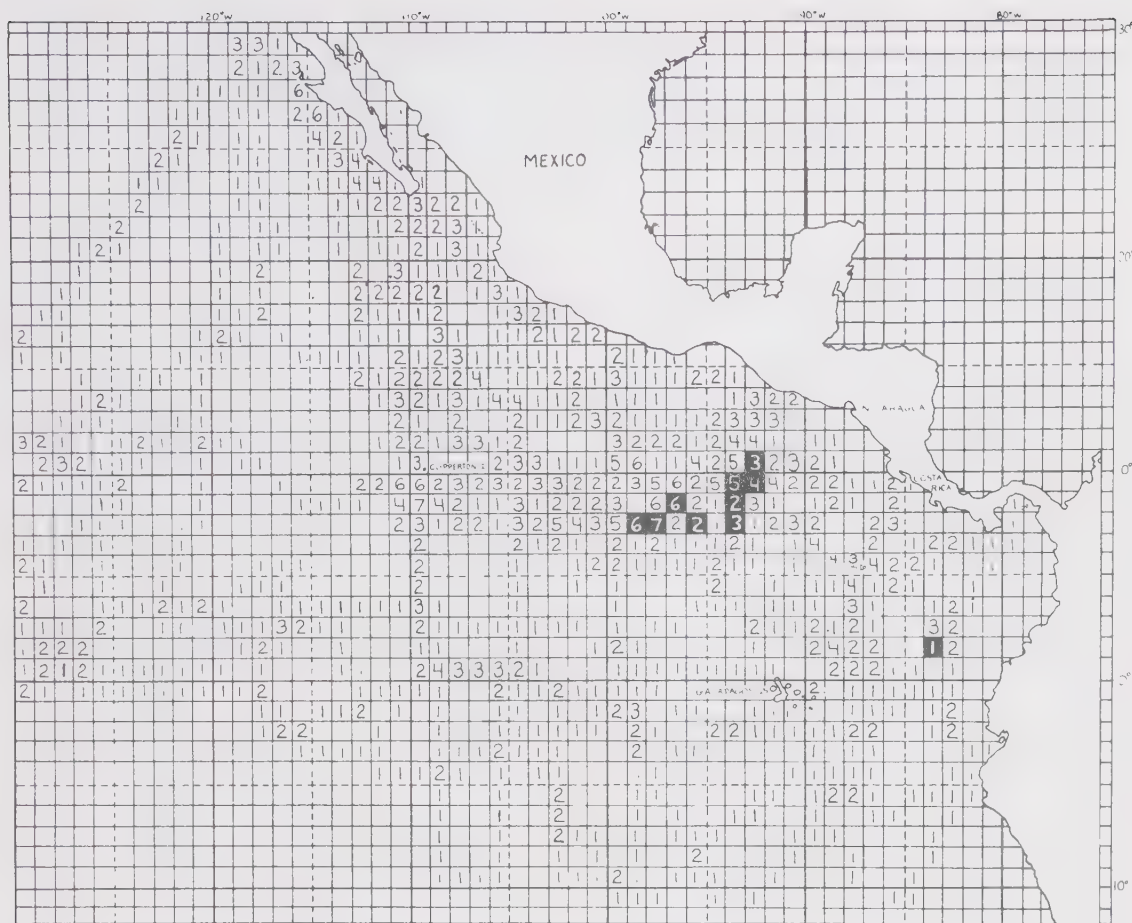


FIGURE 1.—Survey effort for blue whales in the northeastern tropical Pacific over 11 cruises from January to June in 1971, 1975, 1976, and 1977. Each numeral represents the total number of times that vessels entered a 1° block. Darkened blocks indicate blue whale sightings.

fact that blue whales have been sighted in the same general area for three winters indicates that North Pacific blue whales may have a distinct wintering ground to which they migrate each year.

The location of the suggested wintering grounds indicated by the sighting data are lat. 7°29'–10°31'N and long. 95°25'–99°00'W.² Only 1 of the 20 blue whale sightings (lat 1°30'N and long. 83°04'W, 23 January 1975, a solitary individual) was outside of these bounds. The equatorial sighting location of this whale may indicate that either it was not from the North Pacific population, or that North Pacific blue whales do not restrict migration to the hypothetical wintering grounds.

²Cruikshank's observations, in 1928, were also in this area.

Whale Groupings and Behavior

Blue whales are believed to be found singly or in pairs (Leatherwood et al. 1976). In fact, Nemoto (1964) reported that blue whales observed on the summer feeding grounds were solitary. However, five of the sightings reported here were aggregations of whales dispersed over several square miles. Many of the whales were paired. The multiple sightings on 7 February 1975 and 13 February 1976 appear to be mostly of solitary animals (Table 1). However, on both days, no less than 40 n.mi. separated the first and last whales sighted. Also, four out of the five whales observed on 7 February 1975 were headed in a northeasterly direction. This information may indicate that these apparently solitary whales were part of a large dispersed group.

At least one cow and calf were observed and possibly a second pair (Table 1). This is the first actual record of a blue whale calf in the tropics, although historically it has been believed that blue whales have their calves in the warm tropical waters (Mackintosh 1966:126).³

Oceanographic Features

There are several unique oceanographic features which relate to the sighting location of the blue whales. Cromwell (1958) and Wyrteki (1964) discussed the Costa Rican Dome which is located at approximately lat. 9°N, long. 89°W. The dome is apparently a permanent topographic feature (150 km × 300 km) and is formed by the convergence of several major current systems. These currents typically create an area of nutrient transport or upwelling. High standing stocks of zooplankton in the area near the Costa Rican Dome (lat. 7°25'N-10°N) has been reported by several authors (Reid 1962; Blackburn et al. 1970; Holmes⁴). Volkov and Moroz (1977) suggested that the high stable food base of the area creates a habitat suitable for nonmigratory populations of baleen whales. North Pacific blue whales may also use this area for their winter feeding grounds.

In conclusion, the recent sightings of blue whales in the tropics indicates that North Pacific blue whales have a wintering area to which they return each year. Since most of the cruises have occurred largely during the winter months, more information must be collected to determine if whales are found in this area the year round. The high standing stock of zooplankton in this area may indicate that this is a winter feeding area, as well as a calving ground.

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³The average water temperature for 11 sightings was 26.5°C.

⁴Holmes, R. W. 1970. A contribution to the physical, chemical, and biological oceanography of the northeastern tropical Pacific. (Unpubl. manuscript.) Institute of Marine Resources, Scripps Institute of Oceanography, Univ. Calif. La Jolla, Calif. AEC-UCSD-34P99-4.

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Synopsis of Biological Data
on Tunas of the Genus
Euthynnus

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CONTENTS

	Page
Introduction	1
1 Identity	1
1.1 Nomenclature	1
1.11 Valid name	1
1.12 Synonymy	2
1.2 Taxonomy	2
1.21 Affinities	2
1.22 Taxonomic status	4
1.23 Subspecies	6
1.24 Standard common names, vernacular names	6
1.3 Morphology	6
1.31 External morphology	6
*1.32 Cytomorphology	8
1.33 Protein specificity	8
2 Distribution	8
2.1 Total area	8
2.2 Differential distribution	11
2.21 Spawn, larvae, and juveniles	11
2.22 Adults	13
2.3 Determinants of distribution changes	13
*2.4 Hybridization	14
3 Bionomics and life history	14
3.1 Reproduction	14
3.11 Sexuality	14
3.12 Maturity	14
3.13 Mating	15
3.14 Fertilization	15
3.15 Gonads	15
3.16 Spawning	15
3.17 Spawn	21
3.2 Preadult phase	22
3.21 Embryonic phase	22
3.22 Larvae and adolescent phases	23
3.3 Adult phase	31
3.31 Longevity	31
3.32 Hardiness	31
3.33 Competitors	31
3.34 Predators	31
3.35 Parasites, diseases, injuries, and abnormalities	31
3.36 Physiology, biochemistry, etc.	34
3.4 Nutrition and growth	35
3.41 Feeding	35
3.42 Food	36
3.43 Growth rate	36
3.44 Metabolism	38
3.5 Behavior	38
3.51 Migrations and local movements	39
3.52 Schooling	39
3.53 Responses to stimuli	39
4 Population	41
4.1 Structure	41
4.11 Sex ratio	41
4.12 Age composition	41
4.13 Size composition	41
4.14 Subpopulations	46

4.2	Abundance and density (of population)	47
4.3	Natality and recruitment	47
4.31	Reproduction rates	47
*4.32	Factors affecting reproduction	
*4.33	Recruitment	
*4.4	Mortality and morbidity	
*4.5	Dynamics of population	
*4.6	The population in the community and the ecosystem	
5	Exploitation	47
5.1	Fishing equipment	48
5.2	Fishing areas	49
5.3	Fishing seasons	49
5.4	Fishing operations and results	51
*5.41	Effort and intensity	
5.42	Selectivity	51
5.43	Catches	51
*6	Protection and management	
*7	Pond fish culture	
	Literature cited	52

*No information available.

Synopsis of Biological Data on Tunas of the Genus *Euthynnus*

HOWARD O. YOSHIDA¹

ABSTRACT

Biological and fisheries data on *Euthynnus affinis*, *E. alletteratus*, and *E. lineatus* from published and unpublished sources were compiled, synthesized, and summarized following the FAO species synopsis outline.

INTRODUCTION

The fishes of the genus *Euthynnus* are widely distributed in the warm and tropical waters of the world's oceans. In some localities they appear to be the dominant scombrid in the coastal, nearshore waters. *Euthynnus alletteratus* is one of the commonest scombrids in the western North Atlantic (Rivas 1951). In trolling surveys off the southeastern coast of the United States this species was caught most often (Anderson²). Ben-Tuvia (1957) stated that *E. alletteratus* seemed to be the only common scombrid along the coast of Israel in the Mediterranean. In Hawaiian waters *E. affinis* was one of the more common species taken by trolling (Welsh 1949; Tester and Nakamura 1957). Walford (1937) stated that *E. lineatus* was very abundant in the eastern tropical Pacific.

Although the species of *Euthynnus* are widely distributed and apparently abundant in some localities, generally the group as a whole is not commercially as important as the other tunas, e.g., skipjack tuna, *Katsuwonus pelamis*. Calkins and Klawe (1963) stated that *E. lineatus* was of no commercial value and Kikawa and staff (1963) noted that consumer demand for *E. affinis* was not very great in Japan. The world landings of *Euthynnus* ranged from 80,350 to 87,735 metric tons (t) and averaged about 84,674 t during the period from 1973 to 1976 (FAO 1977).

Because the world demand for tuna is steadily growing and since several of the commercially important tunas are at or near the level of maximum sustainable yield, the underexploited and presently commercially unimportant tuna and tunalike species are likely to attract more attention. Therefore it is important that the life history and biology of these species, including *Euthynnus*, be elucidated.

The purpose of this report is to collate and update all the information presently available on *Euthynnus*. All

papers on *Euthynnus* published in the FAO Species Synopsis series (Calkins and Klawe 1963; Kikawa and staff 1963; Marchal 1963; Williams 1963) were relied on heavily in preparing this report.

1 IDENTITY

1.1 Nomenclature

1.11 Valid name

Collette (1978) discussed the relationships of the groups of fishes in the subfamily Scombrinae, including *Euthynnus*. He pointed out that some workers (Fraser-Brunner 1950; Collette and Gibbs 1963) placed the monotypic *Katsuwonus* in synonymy with *Euthynnus*, which he thought obscured the relationships of *Euthynnus* (sensu stricto) with *Auxis* and of *Katsuwonus* with *Thunnus*.

The status of the species within *Euthynnus* is clear; there are three allopatric species of *Euthynnus* throughout the world: *E. affinis* (Cantor) of the Indo-West Pacific, including Hawaii and the Red Sea; *E. alletteratus* (Rafinesque) of the Atlantic Ocean (including the Mediterranean Sea, the Caribbean Sea, and the Gulf of Mexico); and *E. lineatus* Kishinouye of the eastern Pacific.

Euthynnus affinis was originally described as *Thynnus affinis* Cantor 1850. The holotype was from Penang, most likely from the Strait of Malacca. It was 536 mm (FL) long and is preserved as a dried skin in the British Museum as BMNH 1860.3.19.214 (Collette³).

The little tuna from the eastern Pacific was originally described as *Euthynnus lineatus* Kishinouye 1920 and still retains that name.

Euthynnus alletteratus has long been accepted as the valid name of the Atlantic little tuna. It was first described as *Scomber alletteratus* Rafinesque 1810. It was claimed recently by Postel (1973), however, that the fish described and figured by Rafinesque is actually *Auxis rochei* and that the specific name for the Atlantic little tuna should be *Euthynnus quadripunctatus* of Geoffroy

¹Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

²Anderson, W. W. 1954. Progress report, South Atlantic Fishery Investigations, Appendix SA-2. In Atlantic States Marine Fisheries Commission, 13th Annu. Meet., Baltimore, Part 2, p. 211-213.

³B. B. Collette, Systematics Laboratory, National Marine Fisheries Service, NOAA, Washington, DC 20560, pers. commun. March 1978.

Saint Hilaire (1817). However, Tortonese (1975) argued for the retention of the name *alletteratus*. It was also pointed out that Rafinesque (1810) described *Sarda sarda* (as *Scomber palamitus*), *Auxis rochei* (as *S. bisus*), and *E. alletteratus* (as *S. alletteratus*) and that he could not have confused "bisu" (*Auxis*) with "alletterata" (*Euthynnus*) (Tortonese 1976). Thus *Scomber quadripunctatus* of Geoffroy Saint Hilaire (1817) is listed herein as a junior synonym of *Euthynnus alletteratus*.

1.12 Synonymy

The synonymies given below make no distinction between objective and subjective synonyms. The synonymies for *Euthynnus affinis* and *E. alletteratus* are based on synonymies given by Jones and Silas (1964) and Fraser-Brunner (1949), respectively. There are no synonyms for *E. lineatus*.

Euthynnus affinis

- Thynnus affinis* Cantor 1850 (Penang).
Thynnus thunnina. Temminck and Schlegel 1850 (Japan).
Auxis taso (not of Cuvier) Bleeker 1850 (Java).
Euthynnus alletteratus. Jordan, Tanaka, and Snyder 1913 (Japan).
Euthynnus yaito Kishinouye 1923 (Japan).
Gymnosarda alletteratus. Meek and Hildebrand 1923 (Panama).
Wanderer wallisi Whitley 1937 (New South Wales, Australia).
Euthynnus affinis affinis. Fraser-Brunner 1949 (Aden, Seychelles, Thailand).
Euthynnus affinis yaito. Fraser-Brunner 1949 (Japan, Hawaii, Pacific islands).
Euthynnus affinis. Rosa 1950 (in part).
Euthynnus alletteratus affinis. de Beaufort 1951 (in part) (Indo-Pacific).
Euthynnus wallisi. Whitley 1964 (Australia).

Euthynnus alletteratus

- Scomber alletteratus* Rafinesque 1810 (Sicily).
Scomber quadripunctatus Geoffroy Saint Hilaire 1817 (Egypt).
Thynnus leachianus Risso 1827 (Nice).
Thynnus thunnina Cuvier 1829 (Mediterranean).
Thynnus brevipinnis Cuvier and Valenciennes 1831 (Mediterranean).
Thynnus brasiliensis Cuvier in Cuvier and Valenciennes 1831 (Brazil).
Euthynnus alletteratus. Jordan, Evermann, and Clark 1930 (western Atlantic).
Euthynnus thunnina. Nobre 1935 (Portugal).
Euthynnus alletteratus alletteratus. Fraser-Brunner 1949 (North Atlantic).
Euthynnus alletteratus aulolitoralis. Fraser-Brunner 1949 (Gold Coast).

1.2 Taxonomy

1.21 Affinities

— Suprageneric

Phylum Chordata
 Subphylum Vertebrata
 Superclass Gnathostomata
 Class Osteichthyes
 Subclass Actinopterygii
 Order Perciformes
 Suborder Scombroidei
 Family Scombridae
 Subfamily Scombrinae
 Tribe Thunnini

— Generic

Genus *Euthynnus* Jordan and Gilbert 1882.

The generic concept of *Euthynnus* as given below follows that of Godsil (1954a) and Collette (1978).

The species of *Euthynnus* are fusiform, streamlined, and have a lunate caudal fin similar to all tunalike fishes. The body is naked except for the scaly corselet. A series of oblique or longitudinal black markings above the lateral line distinguishes *Euthynnus* from *Katsuwonus*, which has black longitudinal stripes on the belly. The contiguous or nearly contiguous dorsal fins distinguishes *Euthynnus* from *Auxis*, which has widely separated dorsal fins. The concave distal margin of the first dorsal fin separates *Euthynnus* from *Sarda*, which has a nearly straight first dorsal margin. The species of *Euthynnus* usually have eight dorsal and seven anal finlets. Palatine teeth are present in all and vomerine teeth in two of the species. The intestine is straight. There are 37-39 vertebrae. Godsil (1954a) gave a detailed description of the generic skeletal characters.

Unlike *Auxis*, *Euthynnus* has a common trunk for the dorsal and ventral branches of the cutaneous artery. However, *Euthynnus* is more primitive than *Katsuwonus* in that the cutaneous artery's ventral branch is short and dendritic (Godsil 1954a) and much less developed than the dorsal branch. *Euthynnus* also differs from *Auxis* wherein the dorsal cutaneous artery lies dorsal to the corresponding vein and not ventral. In *Euthynnus* the aorta is moved ventrally a distance greater than the depth of the centrum owing to the development of the trelliswork, a distance less than in *Auxis* and more than in *Katsuwonus* (Collette 1978).

— Specific

Euthynnus affinis (Cantor) (Fig. 1).

The following description is based on that given by Godsil (1954a).

The dorsal black markings that are superimposed over a blue to indigo background are most accentuated in the

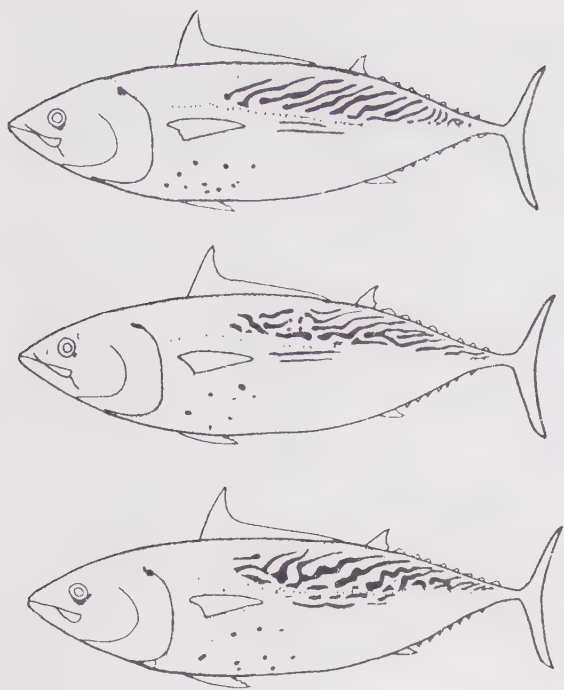


Figure 1.—Variations in the markings of three *Euthynnus affinis*. (From Godsil 1954a, fig. 65.)

anterior region and are more oblique in *E. affinis* than in the other two species. Black or dusky spots are scattered over a relatively wide area on the belly below the pectoral. These spots are variable and cannot be regarded as a specific character.

The crest or rise of the lateral line above the pectoral fin is minimal. The crest or rise, when present, is always gentle at its anterior slope. In many specimens the lateral line is almost horizontal from the opercular margin over the anterior third of the pectoral fin, from where it slopes gently downward.

The caudal keels are not conspicuously developed and are evident externally only by a dorsoventral flattening of the peduncle.

The operculum is relatively straight at the posterior margin and a small dark or black elongated spot is generally present at the dorsal extremity of this margin. The posterior outline of the preoperculum is gently and smoothly rounded. A small irregular dark spot or area is present below the posteroventral margin of the eye.

The maxillary extends to or slightly beyond the vertical through the middle of the eye and, depending on the size of the specimen, 24 to 35 teeth are on each side of the lower jaw. Vomerine teeth are present but palatine teeth, though always present, may not be as prominent.

The dorsal fin is contiguous, is about twice the height of the second dorsal fin, and is roughly half the head length; its dorsal outline is strongly concave. The insertion of the anal fin is on a vertical through the origin of the first dorsal finlet, or between this and the end of the

second dorsal base. There usually are eight dorsal and seven anal finlets.

The gill rakers are fully developed on the first arch only and there is invariably a raker at the angle of the arch including a basal process extending both dorsally and ventrally. The raker count (first arch, left side) is $7(7-9) + 1 + 24(22-24) = 32(29-34)$ (sic). Gill teeth (posterior rakers) are present on all arches and are most developed on the first arch.

Euthynnus alletteratus (Rafinesque) (Fig. 2).

The following description is based on Godsil (1954a).

Euthynnus alletteratus is distinguished from *E. affinis* and *E. lineatus* by the absence of vomerine teeth and by the dorsal markings. The pattern of dorsal markings includes broken, longitudinal black or dark bars running irregularly from the corselet towards the caudal region and are more continuous and regular posteriorly. Anteriorly, short irregularly curved lines, blotches, or spots, replace the bars.

The markings are superimposed over a background of blue which shades dorsally into the deep blue and black of the middorsal line. The blue fades into silver below the lateral line and the entire belly is silvery or dusky; an irregular number of black or dark spots are present between ventral and pectoral fins, and slightly posterior to the pectorals.

The ventral projection of the corselet is variable but generally short, extending posterior to the tip of the pectoral, a distance not exceeding one-fourth (or occasionally more) the length of the pectoral fin in most specimens. The maxillary extends posteriorly to a vertical drawn through the middle of the eye.

The posterior margin of the operculum is relatively straight and the preoperculum smoothly rounded. The teeth are moderate, individually distinct, and number from approximately 25 to 35 on each side of the lower jaw. The palatine teeth are sharp and conspicuous.



Figure 2.—Variations in the dorsal markings of *Euthynnus alletteratus*. (From Fraser-Brunner 1949, fig. 2.)

The following description is also based on Godsil (1954a).

This species can in most instances be readily identified by the dorsal markings, which generally consist of a series of three, four, or five broad continuous black stripes running horizontally on the back from the corselet to the caudal fin. The most ventral stripe starts anteriorly below the lateral line and generally crosses it in its path to the caudal region. Variations in the pattern consist mainly of interruptions in the continuity of the

stripes, or branching of individual stripes including supplementary short irregular markings between.

The black dorsal stripes are superimposed over a background of blue that deepens into black dorsally and shades into grey and silver below. The belly is dusky or silvery; an irregular number (usually from two to six) of black spots are present between the pectoral and pelvic fins.

Palatine teeth are present in all specimens; vomerine teeth are present although difficult to discern in some specimens.

The posterior margin of the operculum is straight and the free margin of the preoperculum is smoothly rounded. The maxillary extends to a vertical drawn through the center of the eye.

A key for the separation of the species of *Euthynnus*, as adapted from Godsil (1954a), is given below.

A. Specimens having 37 (36-38) vertebrae, with four lobes or protuberances on each of two vertebrae, predominantly the 31st and 32d. (Invariably has vomerine teeth; usually has about five continuous, horizontal black dorsal stripes; 33 to 39 gill rakers and 29 to 31 gill teeth.) *E. lineatus*

B. Specimens having 39 vertebrae.

1. Vomerine teeth present. No indication of lobes on 33d or 34th vertebrae. (Usually has oblique broken dorsal markings; from 29 to 33 gill rakers and 28 or 29 gill teeth.) *E. affinis*
2. Vomerine teeth absent, although a longitudinal bony ridge can be felt in this area. Incipient lobes or protuberances occur on the 32d and 34th vertebrae. (Usually has broken horizontal dorsal markings; from 37 to 40 gill rakers and 31 or 32 gill teeth; width of snout between anterior margin of eyes less than distance of this plane from tip of upper jaw.) *E. alletteratus*

1.22 Taxonomic status

See also section 1.11.

Godsil (1954a) made a detailed comparison of the three species of *Euthynnus* (Table 1). He indicated that while the specific identity of *E. affinis*, *E. alletteratus*, and *E. lineatus* appeared to be well established, most of the differences that distinguish each species were relative. He noted that all the characters that positively separate the species were skeletal and that only the absence of the dentigerous vomerine plate in *E. alletteratus* could be used for superficial identification. However, it should be pointed out that *E. alletteratus* (37-40) is separable from *E. affinis* (29-33) on the basis of gill raker counts.

Euthynnus lineatus is clearly separated from *E. affinis* and *E. alletteratus* by having 37 (36-38) vertebrae as op-

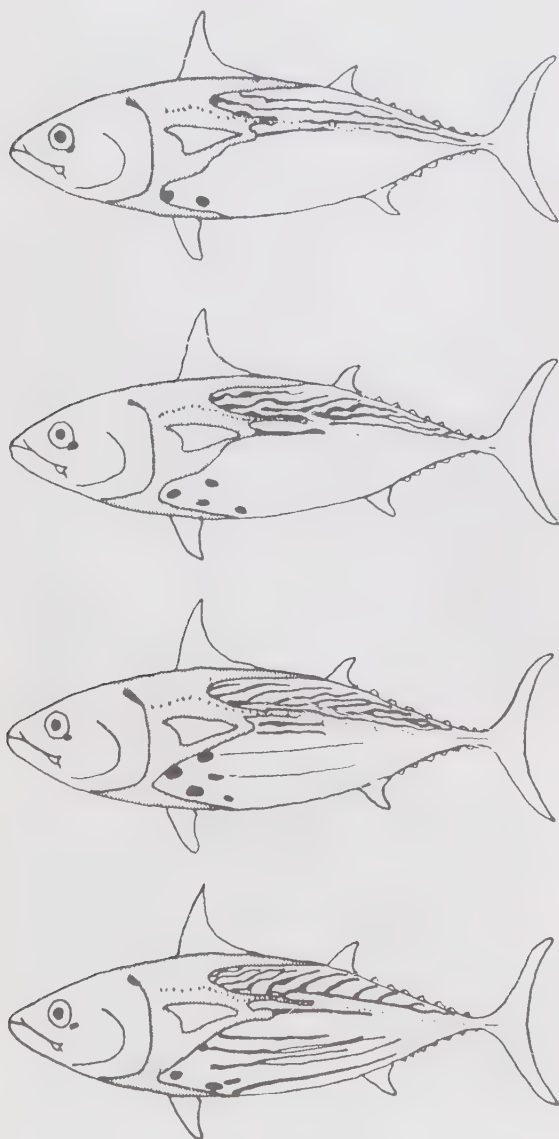


Figure 3.—Variations in the dorsal markings of *Euthynnus lineatus*. Upper figure represents the typical pattern and the lowest figure shows an extreme variant. (From Godsil 1954a, fig. 56.)

Table 1.—Tabular comparison and evaluation of suggestive differences in three species of *Euthynnus*. (From Godsil 1954a, table 17.) The terms used under the column, "nature of difference" are subjective and were not precisely defined by Godsil.

Character	<i>E. lineatus</i>	<i>E. alletteratus</i>	<i>E. affinis</i>	Nature of difference
External				
Dorsal markings	Continuous, horizontal bars	Broken horizontal bars	Broken oblique bars	Indicative
Color	Darker or deeper hued than in <i>alletteratus</i> or <i>affinis</i>	As in <i>affinis</i>	As in <i>alletteratus</i>	Relative
Belly spots	Larger than in <i>affinis</i>	Not recorded	Consistently smaller than in <i>lineatus</i>	Relative
Lateral line	a. Dip below second dorsal b. Relatively steep rise above pectoral	No dip below second dorsal Gentle rise above pectoral	No dip below second dorsal No pronounced rise above pectoral	Indicative Relative
Vomerine teeth	Present	Absent	Present	Positive
Maxillary extent	To vertical through center of eye	As in <i>lineatus</i>	To or beyond vertical through center of eye	Indicative
Proportions:				
Head length	3.13 to 3.62, as in <i>affinis</i> , longer than <i>alletteratus</i>	3.65 to 3.89, shorter than <i>affinis</i> and <i>lineatus</i>	3.44 to 3.60, as in <i>lineatus</i> , longer than <i>alletteratus</i>	Biometrical
Insertion				
1st dorsal	2.82 to 3.33, more posterior than <i>alletteratus</i> , as in <i>affinis</i>	3.37 to 3.55, more anterior than in <i>affinis</i> and <i>lineatus</i>	3.11 to 3.23, as in <i>lineatus</i> , more posterior than in <i>alletteratus</i>	Biometrical
2d dorsal	1.51 to 1.79, includes <i>affinis</i> and <i>alletteratus</i>	1.72 to 1.77, as in <i>lineatus</i> , more anterior than in <i>affinis</i>	1.65 to 1.70, as in <i>lineatus</i> , more posterior than in <i>alletteratus</i>	Biometrical
anal fin	1.37 to 1.55, as in <i>affinis</i> , more posterior than in <i>alletteratus</i>	1.57 to 1.61, more anterior than in <i>affinis</i> and <i>lineatus</i>	1.48 to 1.52, as in <i>lineatus</i> , more posterior than in <i>alletteratus</i>	Biometrical
ventral fin	2.76 to 3.25, as in <i>affinis</i> , more posterior than in <i>alletteratus</i>	3.27 to 3.46, more anterior than in <i>affinis</i> and <i>lineatus</i>	3.07 to 3.24, as in <i>lineatus</i> , more posterior than in <i>alletteratus</i>	Biometrical
Ventral insertion to vent	2.62 to 3.01, includes <i>affinis</i> and overlaps <i>alletteratus</i>	2.57 to 3.12, overlaps <i>lineatus</i> less than <i>affinis</i>	2.75 to 2.95, as in <i>lineatus</i> , greater than <i>alletteratus</i>	Biometrical
Width between anterior margin of eye	Less than distance from tip of upper jaw to plane through anterior margin of eye	Less than distance from tip of upper jaw to plane through anterior margin of eye	Greater than distance from tip of upper jaw to plane through anterior margin of eye	Biometrical
Gill rakers	7 to 10 +1 +24 to 28 Total count 33 to 39	10 to 11 +1 +26 to 28 Total count 37 to 40	7 to 8 +1 +22 to 24 Total count 29 to 33	Biometrical
Gill teeth	8 to 10 +21 to 23 Total count 29 to 31	9 +22 to 23 Total count 31 to 32	8 +20 to 21 Total count 28 to 29	Biometrical
Anal rays	11 to 12	11 to 15	13 to 14	Biometrical
Internal				
Ventral view of viscera				
1. Mosaic	Absent	Absent	Present, generally	Indicative
2. Right lobe of liver	Lateral, as in <i>affinis</i>	Mesial	Lateral, as in <i>lineatus</i>	Doubtful
3. Fat organ	Absent	Absent	Present, generally	Indicative
Ureter				
1. Branches	Large, straight, few collecting tubules as in <i>affinis</i>	Generally small, erratic, numerous collecting tubules	Large, straight, few collecting tubules as in <i>lineatus</i>	Relative—questionable
Skeleton				
Vertebral column	37 vertebrae	39 vertebrae	39 vertebrae	Positive
Protuberances	4 large lobes on each, 31st and 32d vertebrae	Incipient lobes on 33d and 34th vertebrae	No trace	Positive

posed to 39. It is further differentiated by the presence of four characteristic lobes on each of the 31st and 32d vertebrae and by having the major portion of the caudal bony keel on these two vertebrae. The major portions of the caudal bony keels are on the 33d and 34th vertebrae in *E. affinis* and *E. alletteratus*.

Euthynnus affinis and *E. alletteratus* are specifically different in several structural features: the absence of vomerine teeth in *E. alletteratus*, the presence of incipient

lobes on the 33d and 34th vertebrae in *E. alletteratus* and their absence in *E. affinis*. Identification of *E. affinis* and *E. alletteratus* could be made by the presence of vomerine teeth, together with the broken oblique dorsal markings in *E. affinis* and the broken horizontal markings in *E. alletteratus*, and the number of gill rakers.

Godsil (1954a) also noted that *E. affinis* differed slightly from *E. alletteratus* in many of the body proportions. In summing the ratios resulting from dividing the body

length (fork length) in each case by the head length, first dorsal insertion, second dorsal insertion, anal insertion, and ventral insertion, he obtained figures ranging from 12.86 to 13.23 for *E. affinis* (eight specimens 378-643 mm

FL) and 13.64 to 14.19 for *E. alletteratus* (seven specimens 503-763 mm FL). He found that these values were independent of fish size for both species so that mean values, 13.046 for *E. affinis* and 13.996 for *E. alletteratus*, could be used to define the species. The head of *E. affinis* was proportionately larger and the fins were more posteriorly inserted.

Table 2.—Common and vernacular names of *Euthynnus affinis*, *E. alletteratus*, and *E. lineatus*.

Country	Standard common name(s)	Vernacular name(s)
<i>Euthynnus affinis</i>		
Australia	Mackerel tuna, little tuna	—
Sri Lanka	Lesser bonito, mackerel tuna	Atavalla, Ragodura, Sureya (Sinhalese), Shurai (Tamil)
China	—	Tow chung
Comoro Island	Bonito	Mibassi, Mpassi
East Africa	Bonito, little tuna	Sehewa (Kiswahili)—also refers to <i>Auxis</i> spp. and <i>Katsuwonus pelamis</i>
Hawaii, U.S.A.	Little tuna	Bonito, kawakawa
India	—	Choori min, suraly (Tamil); ohaman, chuki (Marathi)
Indochina	—	Ca ngu
Indonesia	—	Tongkol, diverg-bonito, tongkol komo, poetilai
Japan	Yaito	Suma, hiragatsuwo, obosogatsuwo segatsuwo, sumagatsuwo, watanabe
Madagascar	Bonite	Thonnine
Malaysia	—	Tongkol; Ikanayer, Sembak, Choreng, Kembel-mas, Tombal-mas (Malay)
Mauritius	Bonito	Bonite
Mirjurtein coast	—	Shirwa, shirwi (Arabic)
Mogadiscio	—	Maba'adi (Somali); Jeidha (Somali), also refers to small <i>Thunnus albacares</i> and <i>Megalaspis cordyla</i>
New Guinea	Kababida	—
Pakistan (West)	Dwarf bonito	Dawan, Chooki, Jukko
Philippines	Oceanic bonito	Katsarita, turingan, yaito bonito
Seychelles	Little tunny, bonito	Bonite
Somalia	—	—
<i>Euthynnus alletteratus</i>		
Abidjan	Bonita	—
Angola	—	Merma
France	Thonine	—
Ghana	—	El'la (Apollonien), Poponkou (Keta)
Guinea	—	Makreni
Ivory Coast	—	Klewe (Kru), bokou-bokou (Alladian)
Mauritania	—	Corrinelo (Vermeulen)
Portugal	Atun	Fule-fule
Senegal	—	Walaz (Ouolof), dolo-dolo (Lebau)
South Africa	Little tunny, little tuna, mackerel tuna	Merma
Spain	Bacoreta	—
Tunisia	—	R'zem
United States	Little tunny	False albacore
<i>Euthynnus lineatus</i>		
Ecuador	—	Negra, bonito negro
Mexico	—	Barrilete negro
Peru	—	Barrilete negro
United States	Black skipjack	Cross-bred mackerel

1.23 Subspecies

No subspecies are recognized.

1.24 Standard common names, vernacular names

The common and vernacular names of the three species of *Euthynnus* are given in Table 2.

1.3 Morphology

1.31 External morphology

The pattern of markings may vary, sometimes considerably, in the three species of *Euthynnus* (Fraser-Brunner 1949; Godsil 1954a). (See Figs. 1-3.)

Euthynnus affinis

Godsil (1954b) made morphological studies on *E. affinis* from Hawaii and Japan (Table 3). He found several minor differences in the body proportions of fish from the two areas but concluded that these differences merely indicated population differences.

Meristic data on *E. affinis* from various areas are given in Table 4.

Table 3.—Body proportions of *Euthynnus affinis* from Japan and Hawaii. (From Godsil 1954b, table 1.)

Proportions	Range in ratios	
	Japan	Hawaii
Head length	3.66-3.72	3.44-3.60
1st dorsal insertion	3.07-3.27	3.11-3.23
2d dorsal insertion	1.64-1.67	1.65-1.70
Anal insertion	1.53-1.54	1.48-1.52
Ventral insertion	3.33-3.43	3.07-3.24
Greatest body length	—	3.55-3.99
Dorsal-ventral distance	3.97-4.18	3.86-4.18
Dorsal-anal distance	2.31-2.37	2.28-2.38
Ventral insertion to vent	2.75-2.86	2.75-2.95
Length of 1st dorsal base	3.24-3.41	3.23-3.53
Length of 2d dorsal base	14.07-15.96	14.29-15.53
Length of anal base	13.76-14.46	14.02-17.38
Pectoral length	6.23-6.88	5.54-6.05
Height of 1st dorsal	6.86-7.00	6.41-7.00
Height of 2d dorsal	13.83-14.78	12.10-14.15
Height of anal	13.83-15.00	11.91-14.15
Diameter of iris ¹	7.27-7.82	6.06-8.00
Maxillary length ¹	2.49-2.53	2.31-2.51
Snout to posterior margin of eye ¹	2.35-2.38	2.14-2.34

¹ Ratio of this measurement is to head length. All other measurements are related to fork length.

Table 4.—Enumerative data on *Euthynnus affinis*.

Area	First dorsal fin	Second dorsal fin	Dorsal finlets	Anal fin	Anal finlets	Pectoral fin	Gill rakers
Sri Lanka							
Deraniyagala (1952)	14-15	12	8	14-15	7	28	22-24 (lower arch)
Munro (1955)	15	20	8	14	7	26	24 (lower arch)
East Africa							
Morrow (1954)	14-15	11-12	8	12-14	6-7	—	—
Williams (1956, 1964)	15-16	11-13	8	13-14	6-7	—	(7-10) + (22-23) = 29-33
India							
Jones and Silas (1964)	14	11-14	8-9	12-15	6-8	24-28	(7-10) + (22-25) = 29-35
Indonesia							
De Beaufort and Chapman (1951)	15	13	8	14	7	24	24 (lower arch)
Indo-Pacific							
Fraser-Brunner (1949, 1950)	—	—	—	—	—	—	(7-10) + (22-23) = 29-33
Madagascar							
Fourmanoir (1957)	15	11-13	8	13-15	7-8	—	25 (lower arch)
[Pakistan.] (west)							
Central Fish Department (1955)	15	13-14	8	14	8	26	—
Red Sea							
Steinitz and Ben-Tuvia (1955)	15-16	—	8-9	—	7	—	23-24 (lower arch)
Reunion							
Blanc and Postel (1958)	—	—	—	—	—	—	8+1+24 = 33
South Africa							
Smith (1961)	15-16	11-13	8	12-15	6-8	—	25 (lower arch)
Japan							
Godsil (1954b)	15	12-13	8	14	7	—	8+1+(22-24) = 31-33
Hawaii							
Godsil (1954b)	14-15	12-13	8	13-14	7	—	(7-9)+1+(22-24) = 29-34

Euthynnus alletteratus

Based on body proportions of *E. alletteratus* taken along the eastern Atlantic, Marchal (1963) indicated that there were no noteworthy differences in the samples from Cap Vert, Senegal, to Ghana.

Postel (1956) compared body proportions and meristic data of *E. alletteratus* from the Mediterranean Sea (Tunisia) and the eastern Atlantic Ocean (Senegal). He noted that the Tunisian sample was characterized by a shorter head and a shorter predorsal (snout to insertion of first dorsal) and preventral (snout to insertion of ventral) distance (Table 5). The Tunisian specimens also had a smaller number of gill rakers (36-41) than the Senegalese specimens (<38-47).

Body proportions of *E. alletteratus* from the U.S. Atlantic coast are given by Godsil (1954a) (Table 6). He also presented meristic data from these fish, which are shown below.

Meristic character	Counts
First dorsal spines	10-15
Second dorsal rays	12-13

Dorsal finlets	8
Anal rays	11-15
Anal finlets	7
Gill rakers	(10-11) + (0-1) + (26-28) = 37-40

Mansueti and Mansueti (1962) prepared a "topographic" osteology of a specimen captured in Chesapeake Bay (Fig. 4).

Euthynnus lineatus

Body proportions of *E. lineatus* are given in Table 7. Meristic data, from Godsil (1954a), are given below.

Meristic character	Counts
First dorsal spines	13-15
Second dorsal rays	11-12
Dorsal finlets	8-9
Anal rays	11-13
Anal finlets	7-8
Gill rakers	(7-11) + 1 + (23-29) = 31-41

Table 5.—Body proportions of *Euthynnus alletteratus* from Tunisia and Senegal (Postel 1955b: 132-133; 1956: 54). Ratios indicate fork length divided by length of body parts.

Length class (cm)	N	Ratios			
		Head length	First dorsal insertion	Ventral insertion	Pectoral length
Tunisia					
40-45	1	4.27	3.40	3.40	7.06
45-50	2	4.21	3.57	3.48	6.99
50-55	11	4.22	3.50	3.46	6.99
55-60	30	4.24	3.55	3.50	6.95
60-65	10	4.29	3.56	3.53	6.90
65-70	16	4.28	3.53	3.53	6.70
70-75	13	4.29	3.55	3.53	6.82
75-80	3	4.21	3.59	3.55	6.86
80-85	5	4.29	3.60	3.57	6.88
85-90	5	4.33	3.58	3.55	6.88
90-95	3	4.40	3.67	3.59	6.81
95-100	1	4.37	3.65	3.62	7.06
Senegal (Males)					
30-35	1	3.82	3.25	3.15	—
35-40	7	3.84	3.28	3.18	6.12
40-45	81	3.85	3.30	3.20	6.08
45-50	62	3.85	3.30	3.22	6.14
50-55	13	3.87	3.33	3.24	6.31
55-60	0	—	—	—	—

1.33 Protein specificity

The erythrocytes of two *E. lineatus* were tested with a series of 540 bean extracts as part of a preliminary work on a program for typing fish blood. On the basis of agglutinations, it was determined that the blood of *E. lineatus* can be differentiated from that of six other scombrids in the eastern tropical Pacific (Calkins and Klawe 1963).

Table 6.—Body proportions of seven *Euthynnus alletteratus* from the western Atlantic (Atlantic coast of United States). Fork length the numerator except those indicated by an asterisk, where head length is the numerator. (From Godsil 1954a, table 15.)

Proportions	Ratios
Head length	3.65-3.89
1st dorsal insertion	3.37-3.55
2d dorsal insertion	1.72-1.77
Anal insertion	1.57-1.61
Ventral insertion	3.27-3.46
Greatest body depth	3.91-4.16
Greatest body width	6.07-6.12
Dorsal-ventral distance	4.08-4.36
Dorsal-anal distance	2.37-2.50
Ventral insertion to vent	2.87-3.12
Length of first dorsal base	3.30-3.57
Length of second dorsal base	14.16-17.25
Length of anal base	13.80-16.05
Pectoral length	5.89-6.50
Height of 1st dorsal	6.90-7.74
Height of 2d dorsal	10.78-13.55
Height of anal	10.78-12.74
Diameter of iris	*7.81-8.35
Maxillary length	*2.54-2.74
Snout to posterior margin of eye	*2.43-2.45

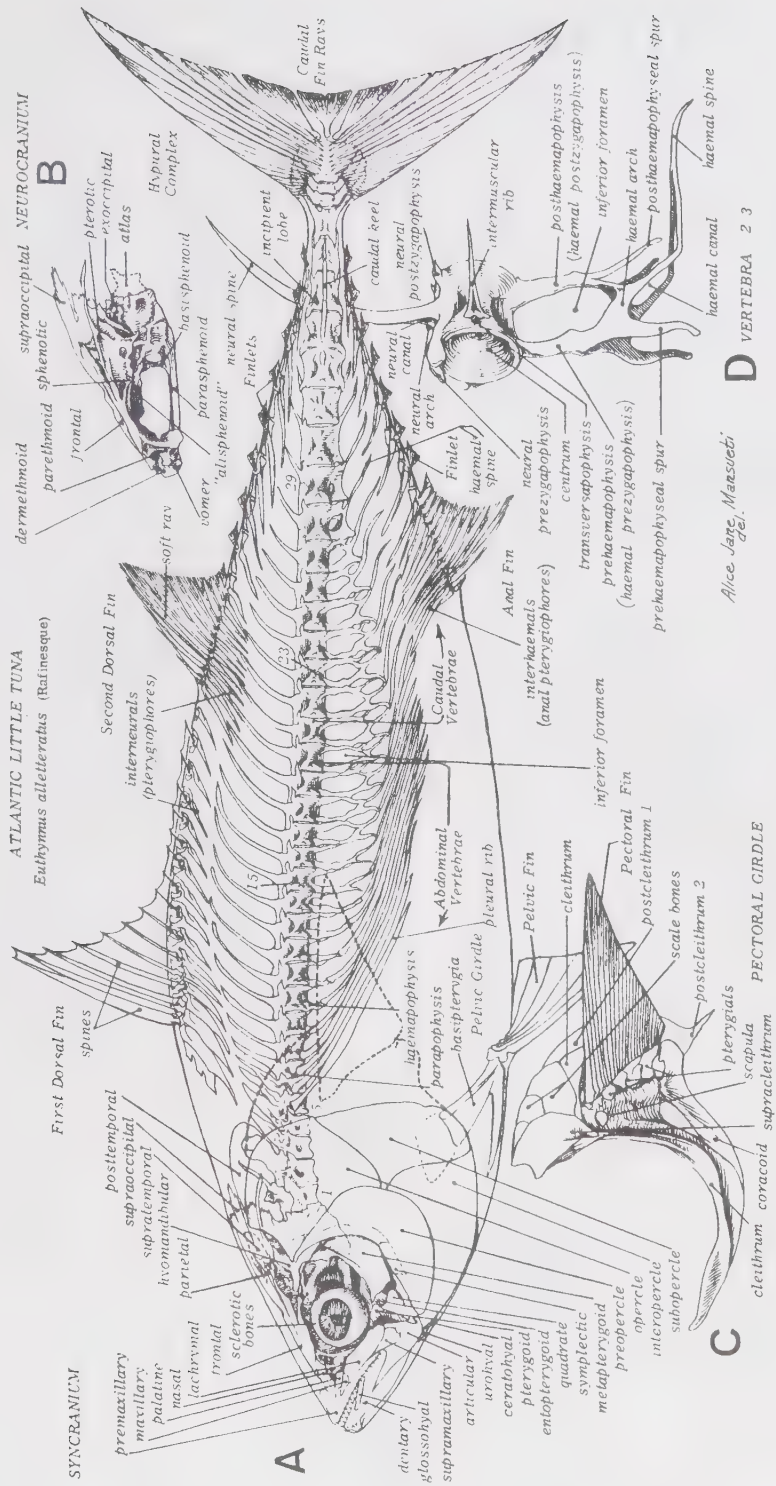
2 DISTRIBUTION

2.1 Total area

In general the species of *Euthynnus* are coastal fishes found in tropical and subtropical waters of the world. Of the three species, *E. lineatus* has the most restricted distribution, occurring only in the eastern tropical Pacific Ocean. *Euthynnus affinis* and *E. alletteratus* are

Table 7.—Measurements (millimeters) and proportions of *Euthynnus lineatus*. Fork length the numerator except those indicated by an asterisk, where head length is the numerator. (From Godsil 1954a, table 10.)

Proportions	Fish number																	Ratios
	19	20	24	26	28	29	30	31	32	33	34	35	36	37	38			
Body length	520	574	583	492	472	446	427	613	514	432	476	455	484	ca. 443	462			
Head length	150	167	170	157	137	138	123	176	148	116	136	132	137	132	134	3.13- 3.72		
1st dorsal insertion	165	186	183	Broken	150	158	133	197	160	129	146	142	145	145	143	2.82- 3.35		
2d dorsal insertion	306	345	340	326	283	293	252	367	299	249	278	267	280	ca. 269	272	1.51- 1.79		
Anal insertion	336	384	386	359	308	315	281	408	339	280	305	295	316	292	302	1.37- 1.56		
Ventral insertion	164	182	—	178	154	153	137	198	167	132	153	146	168	147	154	2.76- 3.27		
Greatest body depth	132	157	—	148	ca. 123	131	—	—	128	—	—	—	—	—	—	3.32- 4.58		
Greatest body width	ca. 85	—	—	—	ca. 79	—	—	—	ca. 85	—	—	—	—	—	—	5.93- 6.17		
Dorsal-ventral distance	128	147	—	—	116	127	—	—	120	—	—	—	—	—	—	3.51- 4.55		
Dorsal-anal distance	210	241	—	—	192	204	—	—	210	—	—	—	—	—	—	2.19- 2.50		
Ventral insertion to vent	180	206	—	187	157	170	144	205	175	147	149	153	153	143	150	2.62- 3.19		
Length 1st dorsal base	146	168	—	Broken	137	143	—	—	145	—	—	—	—	—	—	3.12- 3.86		
Length 2d dorsal base	32	33	—	—	30	34	—	—	31	—	—	—	—	—	—	13.12-18.84		
Length of anal base	31	31	—	—	24	30	—	—	31	—	—	—	—	—	—	14.87-20.10		
Pectoral length	84	88	—	89	78	84	—	—	87	—	—	—	—	—	—	5.31- 6.99		
Height of 1st dorsal	66	72	—	Broken	64	71	—	—	76	—	—	—	—	—	—	6.28- 7.97		
Height of 2d dorsal	33	Broken	—	—	33	35	—	—	36	—	—	—	—	—	—	12.74-16.63		
Height of anal	34	ca. 45	—	—	36	35	—	—	35	—	—	—	—	—	—	12.74-18.29		
Diameter of iris	23	ca. 20	—	20	—	20	—	—	19.5	—	—	—	—	—	—	* 6.00- 7.85		
Maxillary length	59	65	—	57	53	52	—	—	57	—	—	—	—	—	—	* 2.48- 2.75		
Snout to posterior margin of eye	—	—	—	—	ca. 58	—	—	—	62	—	—	—	—	—	—	* 1.97- 2.39		



more widely distributed in the world's oceans. The geographic classification and codes from Rosa (1965) were used in part to describe the distribution of the species.

Euthynnus affinis
ISEW (Indo-Pacific, central)
ISW (Indian Ocean)

100 Africa. 120 northeastern area; 130 eastern central area; 156 Malagasy Republic.

400 Asia. 420 central area; 430 southeastern area; 440 eastern area (mainland); 450 eastern area (is.).

600 Oceania. 610 Australia; 640 eastern Oceania; 660 U.S.A. (Hawaii); 670 Pacific Is.; 680 central groups.

Euthynnus affinis is widely distributed in the warm waters of the Indo-Pacific region (Fig. 5). In the western Pacific it is found from the coast of southern Japan, throughout the Ryukyu Islands, Taiwan, along the coast of Indochina, the Philippines, and around Borneo and New Guinea (Kikawa and staff 1963). Whitley (1964) reported its occurrence (as *Euthynnus wallisi*) along the west, north, and east coasts of Australia. It also occurs around oceanic islands of the Pacific including the east and west Carolines and the Marshall Islands (Kikawa and staff 1963), the Gilbert Islands (Randall 1955), the Hawaiian Islands, Midway (Chapman 1946), the Line Islands and the Marquesas Islands, New Caledonia and New Hebrides (Angot 1959), and Tahiti (Herre 1932). A stray *E. affinis* was recorded from Los Angeles Harbor, Calif. (Fitch 1953). No exhaustive search of the literature was made for records of *E. affinis* in the Pacific Ocean. However, the records listed herein suggest that *E. affinis* may have a wider distribution than indicated here and in Figure 5.

In the Indian Ocean the distribution of *E. affinis* is essentially continuous along the entire east African coast including the Red Sea and the Gulf of Aden, along the coast of Pakistan and both coasts of India, Burma,

Malaysia, and Indonesia, and to the west coast of Australia. It occurs around Madagascar (Malagasy Republic), Sri Lanka (Ceylon), and the offshore islands and archipelagos of Mauritius, Reunion, Comoro, the Seychelles including Aldabra, Laccadive, Maldives, and Andaman and Nicobar (Williams 1963; Jones and Silas 1964).

Euthynnus alletteratus
ANW (Atlantic, NW)
ASW (Atlantic, SW)
ANE (Atlantic, NE)
ASE (Atlantic, SE)

100 Africa. 110 northwestern area; 140 western central area; 150 southern area.

200 North America. 236 New England; 237 Middle Atlantic States; 235 southern states; 238 southern Atlantic states.

300 Latin America. 311 Mexico; 320 Caribbean Is.; 351 Brazil; 352 Uruguay; 353 Argentina.

500 Europe. 510 Scandinavia; 520 western area (mainland); 530 British Isles; 540 southern area; 550 southeastern area.

Euthynnus alletteratus is found along both coasts of the Atlantic Ocean and in the Mediterranean Sea. It is also found in the Sea of Marmara and it occurs sporadically in the Black Sea (Demir 1961, 1963) (Fig. 6).

In the eastern Atlantic Ocean, Laevastu and Rosa (1963), in their distributional chart of *E. alletteratus*, indicate that the limits of the "regular" distribution of this species are from off the coast of Morocco to the coast of northwest Africa. Marchal (1963) listed the following areas along the west African coast from which *E. alletteratus* has been recorded: Levrier Bay, Mauritania (Postel 1950); Cape Verde Islands and Gambia (Cadenat 1950; Postel 1950); off the Bissagos, Guinea, and Sierra Leone (Marchal 1961; Postel 1962); the length of the

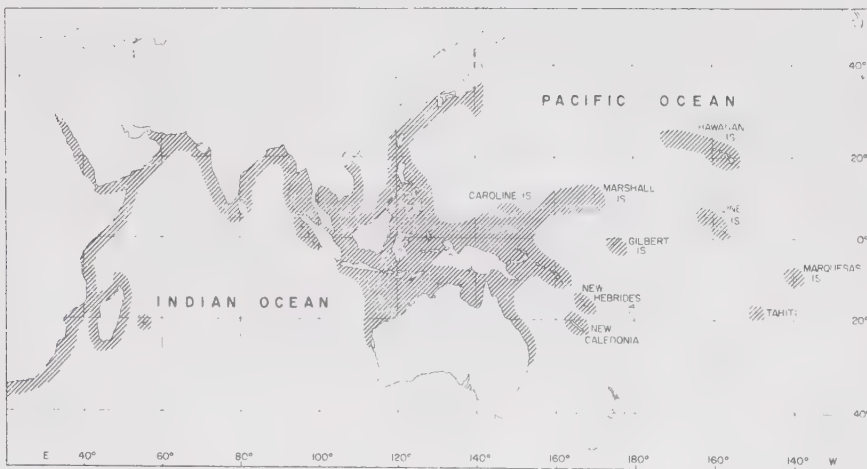


Figure 5.—Distribution of *Euthynnus affinis* in the Indo-Pacific region. (Adapted from Kikawa and staff 1963, fig. 2, and Laevastu and Rosa 1963, fig. 4.)

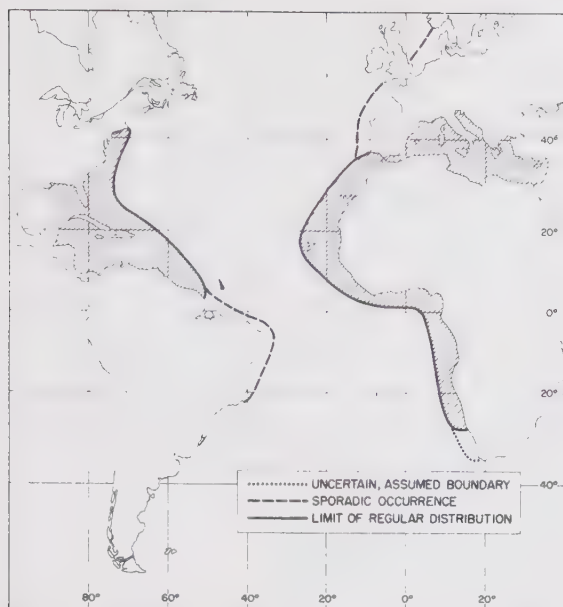


Figure 6.—Distribution of *Euthynnus alletteratus*. (Adapted from Laevastu and Rosa 1963, fig. 4.)

coast of Liberia, the Ivory Coast and Ghana; St. Thomas and Principe Islands (da Costa and Frade 1958); and Pointe-Noire (Roux 1957).

The distributional chart of *E. alletteratus* in the western Atlantic given by Laevastu and Rosa (1963) shows the limits of its distribution from the coast of Maine to the northern boundary of Brazil. Briggs (1958) stated that in the western Atlantic *E. alletteratus* is distributed from "Bermuda and the Gulf of Maine to Ilha Victoria, Brazil, and the northern and eastern Gulf of Mexico." Fraser-Brunner (1949) also recorded the species from Rio de Janeiro, Brazil.

Euthynnus lineatus ISE (Pacific, SE)

200 North America. 232 southwestern states (California).

300 Latin America. 310 Central America (mainland); 340 western South America.

Euthynnus lineatus is found in the tropical coastal waters of the eastern Pacific from about lat. 35°N to 12°S (Fig. 7). Calkins and Klawe (1963) constructed this figure from records of *E. lineatus* reported in the literature, tuna vessel logbooks, scientific logs of oceanographic cruises by ships of the Scripps Institution of Oceanography and the National Marine Fisheries Service, and field-book notes of C. L. Hubbs, Scripps Institution of Oceanography, and D. P. de Sylva, University of Miami. Records of *E. lineatus* in the literature include the northernmost record from off San Simeon, Calif. (lat. 35°20'N, long. 120°40'W) (Nowell 1961), specimens from California waters (Roedel 1948; Fitch 1952), Baja California

(Godsil 1954a), the Tres Marias Islands (Fowler 1944), Acapulco, Mexico (Mais and Jow 1960), Costa Rica (Schaefer and Marr 1948), Colombia Bank (lat. 2°N, long. 79°W), Guayaquil Bank (lat. 3°35'S, long. 80°55'W) (Godsil 1954a; Clemens 1957), and from the Galapagos Islands (Fowler 1938, 1944; Schmitt and Schultz 1940; Seale 1940; Godsil 1954a). Logbooks of commercial tuna vessels indicate that *E. lineatus* has been encountered nearly everywhere along the coastline from about halfway down the coast of Baja California to northern Peru. They have been frequently encountered in the Gulf of California, the Revillagigedo Islands, all along the coast of Mexico and Central America, and the Galapagos Islands. There have been occasional reports of this species from Clipperton and Cocos Islands and there is a single report of its occurrence from Shimada Bank (lat. 16°52'N, long. 117°30'W) (Calkins and Klawe 1963). More recently, they have been recorded as far as 2,000 mi (3,200 km) off the coast in the eastern Pacific (Klawe⁴). In addition there are two records of *E. lineatus* from the Hawaiian Islands (Matsumoto and Kang 1967; Matsumoto 1976).

2.2 Differential distribution

From all indications it appears that the distribution of all the different life stages of *E. affinis* and the other two species of *Euthynnus* appears to be similar. As noted earlier the adults are generally coastal fishes and judging from the distribution of the various life stages of these species, the entire life cycle is completed within the coastal province.

2.21 Spawn, larvae, and juveniles

Euthynnus affinis

Larval and juvenile *E. affinis* are widely distributed in the Indo-Pacific area (Fig. 8). As many investigators have observed in the past, e.g., Matsumoto (1959), it appears that larval and juvenile *E. affinis* are generally taken close to land masses and less frequently around oceanic islands. There also are a few captures of larval fishes in midocean localities but chances are these were carried away from coastal areas by the prevailing currents.

In the coastal waters of southern Japan Yabe et al. (1953) indicate that preadults ranging in length from 150 to 250 mm are taken from August to October near Aburatsu, Kyushu. Preadults also constitute a regular part of the commercial catch in other areas. In the fishery for *E. affinis* off the southwest coast of Sri Lanka, fish smaller than 240 mm appear regularly in the commercial landings (Sivasubramaniam 1970). In the Philippines Wade (1950a) obtained many of his juvenile and preadult *E. affinis* from various fish markets.

⁴ W. L. Klawe, Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography, La Jolla, CA 92037, pers. commun. to Tamio Otsu, National Marine Fisheries Service, Southwest Fisheries Center, Honolulu, HI 96812, November 1977.

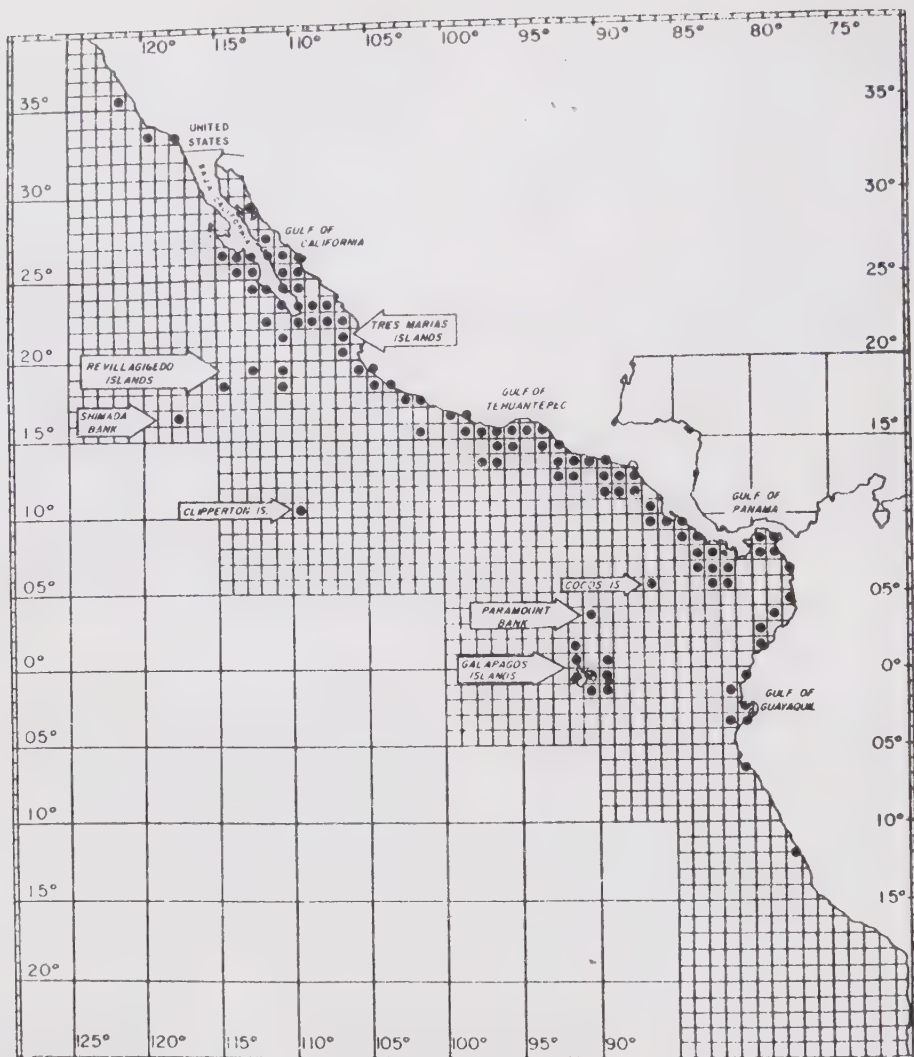


Figure 7.—Distribution of *Euthynnus lineatus* in the eastern Pacific Ocean. (From Calkins and Klawe 1963, fig. 2.)

Euthynnus alletteratus

The distribution of larval and juvenile *E. alletteratus* is shown in Figure 8. They have been recorded from both sides of the Atlantic Ocean, the Mediterranean Sea including the Black Sea and Sea of Marmara, and from the Gulf of Mexico. In the eastern Atlantic along the west African coast, the northernmost record of larval *E. alletteratus* is from off the northern coast of Morocco. There are numerous records of larval *E. alletteratus* from the Gulf of Guinea. The absence of records from farther south along the coast of Africa may merely reflect lack of sampling effort. In the western Atlantic, larval *E. alletteratus* has been collected as far north as lat. 35°42'N off the North Carolina coast of the United States and as far south as lat. 10°S off the coast of Brazil. Although most of the larvae have been collected relatively close to shore,

there are a few midocean records of *E. alletteratus* larvae.

Richards and Simmons (1971) suggested some sort of vertical stratification in the distribution of larval *E. alletteratus*. They noted that the larvae were collected more often at the surface at night. They also tentatively concluded that there was greater net avoidance by larval *E. alletteratus* during the day. However, they attributed the higher frequency of capture at night to vertical migration.

Marchal (1963) stated that along the coasts of the Ivory Coast and Ghana postlarval and juvenile *E. alletteratus* were found at the surface from 2 mi (3.2 km) to around 100 mi (160 km) off the coast. Marchal made the observation that those postlarval and juvenile fish found out to 100 mi (160 km) offshore were probably taken out by the currents because no adults were found beyond the

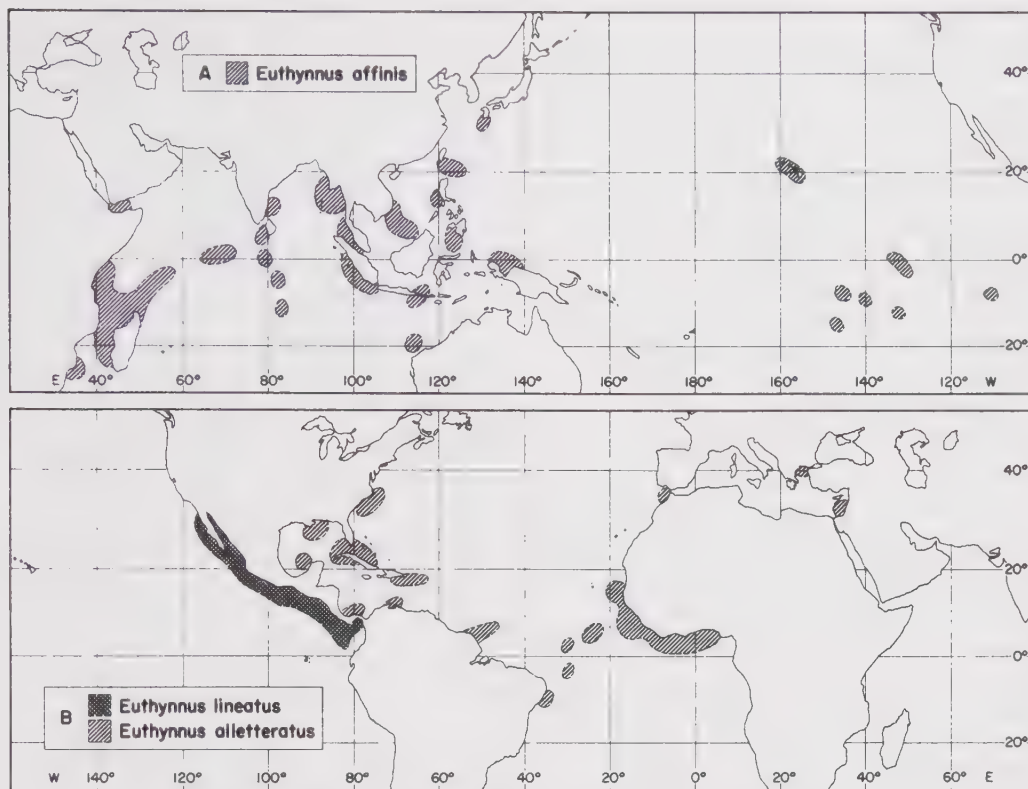


Figure 8.—Distribution of larval and juvenile *Euthynnus* spp. (See Tables 9-11.)

continental shelf. He stated that these young forms of all sizes were taken from October to July and that they may be present all year. Marchal observed that preadult *E. alletteratus* appeared to be closer to the coast than the adults. He indicated that the beach seines did not catch fish over 40 cm long.

In the Mediterranean Sea in Haifa Bay, Oren et al. (1959) captured preadults 80 to 240 mm long from the end of June to the middle of August. Also in the Mediterranean area, Demir (1963) reported the catch of preadult *E. alletteratus* ranging from 145 to 220 mm long in the Sea of Marmara during the period from the last week of August to the second half of September. He also reported 180 to 250 mm long preadults in the Dardanelles from the middle of August to the end of the first week in October.

In the Gulf of Mexico juvenile and preadult *E. alletteratus* 15 to 172 mm long have been commonly found beyond the edge of the continental shelf throughout the summer months (Bullis 1955).

Euthynnus lineatus

Larval and postlarval *E. lineatus* are almost as widely distributed as the adults in the eastern tropical Pacific Ocean (Fig. 8). They have been recorded as far north as lat. 29°45'N (Point Antonio, Baja California) and south

to lat. 04°00'N, long. 81°35'W (the vicinity of Malpelo Island) (Calkins and Klawe 1963). The larvae were also collected near the head and entrance of the Gulf of California. Except for one specimen caught near Malpelo Island, all the larval and juvenile *E. lineatus* have been collected within about 150 mi (240 km) of the mainland.

2.22 Adults

See section 5.3.

2.3 Determinants of distribution changes

The three species of *Euthynnus* seldom occur more than a few hundred miles from land. They are usually found around land masses and island chains generally between lat. 35°N and 35°S (Blackburn 1965). Godsil (1954a) noted that *E. lineatus* along the west coasts of Baja California and Central America appeared to be localized in distribution and confined to certain inshore areas. He also noted that *E. affinis* in the Hawaiian Islands were confined within the 20 or 30 fathom (36.5 or 54.8 m) contour. In the western Pacific near New Guinea *E. affinis* were abundant and distributed in inshore waters throughout the area (Mori et al. 1969). Around the Maldives Islands in the Indian Ocean *E. affinis* are found close to the islands and they often venture into

shallow water in pursuit of bait (Jonklaas 1967). In this respect the species of *Euthynnus* generally appear to be similar to some species of *Sarda* which are also inhabitants of the coastal or neritic, pelagic province. Sverdrup et al. (1942) characterized the neritic province as one where the environment is more variable than in the oceanic. In the neritic province the chemical constituents of the seawater are more variable: salinities are usually lower and some of the inhabitants may be more or less euryhaline.

The species of *Euthynnus*, particularly *E. affinis*, are also found in waters around oceanic islands and archipelagos although here too they are found close to shore. The following example illustrates the type of habitat occupied by the species of *Euthynnus*.

Off the coast of Japan *E. affinis* may occur in waters with salinities ranging from 31.22 to 33.80‰ (Yabe et al. 1953). Yabe et al. (1953) also noted that near Aburatsubo, Japan, heavy autumnal rains make the water turbid 1 or 2 mi (1.6 or 3.2 km) from shore and cause a considerable lowering of the salinity in the surface water. However, these conditions did not seem to affect the catches of *E. affinis*. Kishinouye (1923) noted that *E. affinis* in Japanese coastal waters are found in waters ranging from 18° to 28°C.

Williamson (1970) described the coastal environment of *E. affinis* around Hong Kong. The coast is composed of steep, rocky headlands and islands and the 50 m contour lies about 25 mi (40 km) offshore. The surface water temperature ranges from 14° to 29°C annually. The west side of Hong Kong is greatly influenced by the estuary waters fed by the West River. The bottom in this area is muddy and the water turbid and brackish (surface salinity, 33‰ in February and 6‰ in July). On the east side of Hong Kong more oceanic conditions prevail: the surface salinity is 34‰ in February and 26‰ around July, which is the height of the summer rainy season.

In the Indian Ocean the tropical and subtropical waters are generally characterized by a scarcity of plankton offshore except in areas where vertical mixing of water masses occurs, e.g., off Somalia, where upwelling takes place. Strong development of phytoplankton and the ensuing zooplankton is confined to the immediate coastal areas (Williams 1963).

Along the Atlantic coast of the United States most of the *E. alletteratus* are taken in "green water" and are seldom taken in the "blue water," or slope water of the Florida Current (de Sylva and Rathjen 1961). As de Sylva and Rathjen pointed out, *E. alletteratus* typically occupy the inshore turbid waters. Morice and Cadenat (1952) made a similar observation in Guadeloupe, and Whiteleather and Brown (1945) noted that this species appeared to be a coastal fish in areas around Trinidad, Tobago, and Guyana.

Calkins and Klawe (1963) characterized the general habitats of *E. lineatus* based on published studies (Holmes et al. 1957; Brandhorst 1958; Cromwell 1958; Cromwell and Bennett 1959; Sund and Renner 1959). Calkins and Klawe (1963) noted that *E. lineatus* occurs in the equatorial Pacific water mass which extends

approximately from lat. 23° or 24°N to northern Peru and the Galapagos Islands. There are transition zones to the north and south of the tropical water mass which are influenced by the cold California Current and the Peru Current in the north and south, respectively. The principal warm currents influencing the tropical water mass are the North Equatorial, the Equatorial Counter-current, and the South Equatorial Current. Where *E. lineatus* is most frequently found near the coast, these currents are usually weak and variable and the thermocline is relatively shallow (10-50 m) which allows the exchange of nutrients between the deep layer and the surface waters. In a thermal dome located off Central America (lat. 9°N, long. 90°W) the thermocline is frequently less than 10 m and sometimes reaches the surface. In the Gulf of Panama, the Gulf of Tehuantepec, the Gulf of California, and the inshore waters of Baja California, upwelling enriches the inshore waters.

3 BIONOMICS AND LIFE HISTORY

3.1 Reproduction

3.1.1 Sexuality

All of the species of *Euthynnus* are heterosexual, males and females do not differ in external appearance, and there is no record in the literature of hermaphroditism in these fishes. However, it would not be surprising if hermaphroditic specimens were to occur since cases have been discovered in closely related species, e.g., *Katsuwonus pelamis* (Uchida 1961).

3.1.2 Maturity

Euthynnus affinis

Euthynnus affinis apparently attains sexual maturity at a relatively small size, at least in certain areas of its distributional range. Buñag (1958) examined a total of 30 *E. affinis* 44.4 to 62.2 cm long in Philippine waters and found that the smallest female with mature gonads was a specimen 49 cm long. A 47.7 cm female was found to have spent ovaries. In an earlier study in Philippine waters, a sample of 205 females included a ripe specimen between 40 and 40.9 cm long that was determined to be spent. In yet another study comprising a sample of 144 fish 33.4 to 50.8 cm long, it was found that the smallest mature female was around 38.5 cm long (Ronquillo 1963).

Euthynnus affinis in the Indian Ocean appears to reach sexual maturity later than those occurring in the Philippines. Based on a sample of 75 specimens taken near the Seychelles, Ommanney (1953) reported that *E. affinis* attained sexual maturity between 50 and 65 cm TL (total length), probably in the third year of life. Williams (1956, 1963) examined 37 specimens from east Africa and noted that fish there attained sexual maturity between 55 and 60 cm TL. In Mauritius waters *E. affinis*

55 cm long are mature (Baissac⁶). Off the southwest coast of India near Vizhingam (lat. 08°22'N, long. 76°59'E) the smallest female with ripe ovaries was found to be 48 cm (Rao 1964).

In the South China Sea off Kwangtung, China, *E. affinis* presumably attains sexual maturity at around 50 cm (Williamson 1970). Elsewhere in this paper Williamson also noted that two distinct size-groups of fish made up the spawning schools and that the smaller of the size groups was made up of fish with a mean size of 44 cm which were probably a year old. Around Hawaii, Tester and Nakamura (1957) determined the sex and maturity of 93 *E. affinis* caught by trolling. However, they did not relate the sexual maturity of the fish to its size. They found that five females in their sample were ripe.

Euthynnus alletteratus

In the eastern Atlantic in the area off Dakar, Senegal, Postel (1955b) determined the size of first maturity of *E. alletteratus* as 39.7 cm for the males and 38.6 cm for the females. Postel considered that *E. alletteratus* were sexually mature when the gonadosomatic index reached 3 to 4%, which was related to the time when the sexual products could be expressed by a slight pressure on the body walls. Marchal (1963) stated the smallest *E. alletteratus* he observed in spawning condition were 44.2 to 44.7 cm long off the coast of Guinea.

In the western Atlantic Ocean off the coast of Florida, de Sylva and Rathjen (1961) observed that the smallest fish in ripe condition was a female 27.2 cm long. However, they also noted that most fish in their sample were not in spawning condition until they were 35 cm long. And in the Spanish fishery for *E. alletteratus* based at the southern ports of Barbate and Tarifa, it was found that the size at first spawning was 56.5 cm for the males and 57.0 cm for the females (Rodríguez-Roda 1966).

Euthynnus lineatus

The size at first spawning for *E. lineatus* is not known. There are only fragmentary observations on the gonadal development of this species in the eastern tropical Pacific where it occurs. Mead (1951) reported two females 54.4 and 55.0 cm long, which had swollen and turgid ovaries, from the waters off Central America. Schaefer and Marr (1948) reported two adults from the Gulf of Nicoya, Costa Rica, in an advanced stage of maturity but did not give their size.

3.13 Mating

Although the reproductive behavior of *Euthynnus* has not been positively observed in the natural environment or in experimental tanks and ponds, Hunter and Mitchell (1967) observed a high frequency of wobbling and

chasing by three ripe male *E. lineatus* in a manner similar to that described by Magnuson and Prescott (1966) as reproductive behavior of Pacific bonito, *Sarda chiliensis*. These observations were made by Hunter and Mitchell (1967) near drifting objects under which *E. lineatus* had collected off the coast of Costa Rica. Whether these observations actually represented reproductive behavior by *E. lineatus* remains to be demonstrated.

3.14 Fertilization

Fertilization is external in all the species of *Euthynnus*.

3.15 Gonads

Euthynnus affinis

Information on the fecundity of *E. affinis* is available only from the Indian Ocean. Rao (1964) indicated that *E. affinis* around Vizhingam spawned 210,000 to 680,000 ova per spawning and 790,000 to 2,500,000 ova during the spawning season (Table 8). He noted that the number of ova produced by *E. affinis* increased with the size of the fish.

Table 8.—Fecundity of *Euthynnus affinis* in the Indian Ocean off Vizhingam, India. (From Rao 1964, table 1.)

Fork length (cm)	Weight of fish (kg)	No. of ova per spawning (millions)	No. of ova per spawning season (millions)
48.0	1.37	0.21	0.79
52.5	2.06	0.31	0.88
55.5	2.35	0.30	1.31
58.2	3.20	0.50	2.14
65.0	4.57	0.68	2.50

Euthynnus alletteratus

Not much information is available on the fecundity of *E. alletteratus*. Postel (1955b) determined that the fecundity of a 75 cm fish from off the coast of Dakar, Senegal, was 1,750,000 eggs.

Euthynnus lineatus

The fecundity of *E. lineatus* has yet to be investigated.

3.16 Spawning

Euthynnus affinis

Euthynnus affinis in the Philippines apparently spawn all year round as indicated by the presence of fish in all stages of sexual development throughout the year (Wade 1950b; Buñag 1958). Wade (1950b) stated that his sample was not sufficiently large to discern possible seasonal variations in spawning intensity. Ronquillo (1963) determined the gonad index for a sample of 144 *E. affinis* in

⁶Baissac, J. de B. 1960. Indian Ocean section - genus *Euthynnus*. Mimeogr. rep., 2 p. CCTA/CSA, Colloque sur les Thonides, Dakar, 12-17 Decembre 1960, Tunny (60) 5.

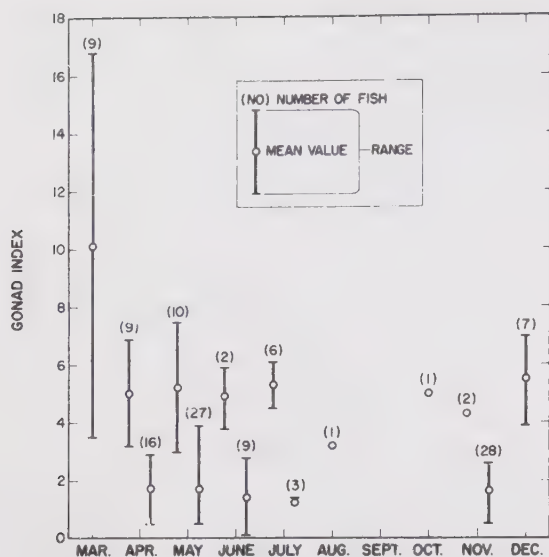


Figure 9.—Seasonal distribution of *Euthynnus affinis* gonad index in the Philippines. (From Ronquillo 1963, table 16.) Gonad index = $\frac{W_o}{L^3} \times 10^3$, where W_o is the weight of the paired ovaries in grams and L is fork length in millimeters.

Philippine waters to define the spawning season (Fig. 9). His results were essentially the same as those obtained by Wade (1950b) and Buñag (1958) in that no clear seasonality in spawning was evident. Ronquillo (1963), however, noted that the highest gonad indices were found from March to May. Based on the development of ovarian ova, Buñag (1958) concluded that *E. affinis* in the Philippines spawns more than one batch of eggs during a spawning season (Fig. 10). Although he did not encounter any fully ripe ovaries in his samples, Buñag (1958) speculated that ripe eggs of *E. affinis* would probably be between 0.8775 and 1.1050 mm in diameter.

On the basis of the distribution of larval *E. affinis* in Philippine waters, Wade (1951) indicated that spawning may have seasonal peaks. Matsumoto (1959), however, indicated that Wade may have misidentified the larvae and that what Wade identified as *E. affinis* were more likely *Auxis*. Based on an earlier study reporting the capture of juveniles, Wade (1950a) stated that *E. affinis* spawn in the vicinity of Manado, Celebes, East Indies; near Marigabato Point, Cotabato Province, Mindanao; and Batangas and Balayan Bays, Luzon, Philippines.

In the western Indian Ocean near the Seychelles, the spawning season for *E. affinis* is during the period of the northwest monsoon, from October–November to April–May including a peak from January to March (Ommanney 1953). Off the coast of east Africa the spawning season extends from January to July, the middle of the northwest monsoon to the beginning of the southeast monsoon (Williams 1963). The capture of larval *E. affinis* in the western Indian Ocean during the months of December and January (Jones and Kumaran 1964) corroborates

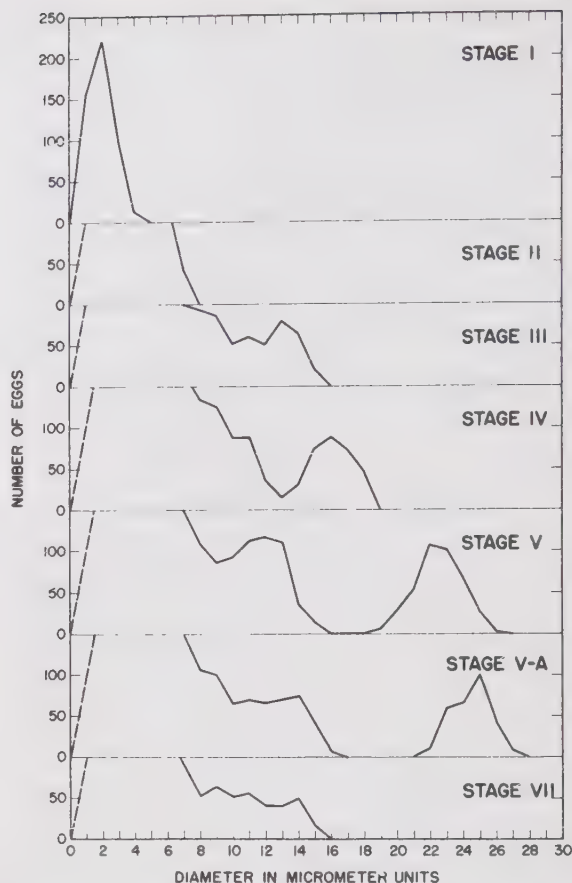


Figure 10.—Ova diameter frequency polygons of *Euthynnus affinis* showing the various stages of development of the ova to maturity: I, immature; II, early maturing; III, late maturing; IV, V, V-A, mature; VI, ripe; VII, spent. (From Buñag 1958, fig. 3.)

the above observations. In other close-by areas in the western Indian Ocean, fish in spawning condition were taken in November and December around Madagascar (Fourmanoir 1957) and in December around Mauritius (Baissac see footnote 5).

Off the southwest coast of India near Vizhanganam, Rao (1964) indicated that *E. affinis* spawns from April to September. He did not discount spawning also in other months of the year and noted the possibility that individual fish may mature and spawn several batches of ova during the spawning season. The capture of juveniles up to 200 mm in the months of January, May, June, September, October, and November near Vizhanganam and Calicut, India (Jones 1960; Table 9) suggests a rather lengthy spawning season for *E. affinis* in these waters.

In the eastern equatorial Indian Ocean, larval *E. affinis* have been captured from August to October in Indonesian waters (Matsumoto 1959; see Table 8) which suggested spawning during these months.

Larval and juvenile *E. affinis* have been recorded from many other areas in the Indo-Pacific (Table 9; see also

Table 9.— Records of larval and juvenile *Euthynnus affinis* in the Indo-Pacific.

Date	Locality		Marine area code [see Rosa (1965)]	Number		Length (mm)	Reference	Remarks
	Lat.	Long.		Larvae	Juveniles			
Apr. 1929	04°03'N	123°26'E	ISEW	1	—	—	Matsumoto (1959)	
	04°03'N	123°26'E		3	—	—	Matsumoto (1959)	
	06°55'N	114°02'E		15	—	—	Matsumoto (1959)	
	06°55'N	114°02'E	ISEW	23	—	—	Matsumoto (1959)	
	06°55'N	114°02'E		25	—	—	Matsumoto (1959)	
	08°02'N	109°36.5'E		1	—	—	Matsumoto (1959)	
	08°02'N	109°36.5'E		2	—	—	Matsumoto (1959)	
May 1929	08°02'N	109°36.5'E	ISEW	42	—	—	Matsumoto (1959)	
	12°15'N	109°26'E		1	—	—	Matsumoto (1959)	
	20°30.5'N	125°28'E		2	—	—	Matsumoto (1959)	
	20°30.5'N	125°28'E	ISEW	2	—	—	Matsumoto (1959)	
June 1929	14°37'N	119°52'E	ISEW	1	—	—	Matsumoto (1959)	
July 1929	00°41.5'S	134°14.5'E	ISEW	1	—	—	Matsumoto (1959)	
	00°41.5'S	134°14.5'E		3	—	—	Matsumoto (1959)	
	00°41.5'S	134°14.5'E	ISEW	2	—	—	Matsumoto (1959)	
	00°40.5'S	134°15'E		7	—	—	Matsumoto (1959)	
	00°40.5'S	134°15'E		3	—	—	Matsumoto (1959)	
	00°40.5'S	134°15'E		10(?)	—	—	Matsumoto (1959)	
	00°40.5'S	134°15'E	ISEW	4	—	—	Matsumoto (1959)	
	00°40.5'S	134°15'E		4	—	—	Matsumoto (1959)	
	00°33'S	134°00'E		11	—	—	Matsumoto (1959)	
	00°33'S	134°00'E		3	—	—	Matsumoto (1959)	
	00°33'S	134°00'E	ISEW	1(?)	—	—	Matsumoto (1959)	
	01°01'S	137°20'E		2	—	—	Matsumoto (1959)	
	01°01'S	137°20'E		3	—	—	Matsumoto (1959)	
	01°20'S	138°42'E		1	—	—	Matsumoto (1959)	
	01°20'S	138°42'E	ISEW	1	—	—	Matsumoto (1959)	
	07°53'S	116°18'E		1	—	—	Matsumoto (1959)	
	07°53'S	116°18'E		2(?)	—	—	Matsumoto (1959)	
	09°09'S	114°47'E		2	—	—	Matsumoto (1959)	
Aug. 1929	06°22'S	105°12'E	ISEW	7(?)	—	—	Matsumoto (1959)	
	06°22'S	105°12'E		13(?)	—	—	Matsumoto (1959)	
Sept. 1929	04°38'S	99°24'E	ISW	1	—	—	Matsumoto (1959)	
	02°00'S	98°59'E	ISW	1	—	—	Matsumoto (1959)	
	02°00'S	98°59'E	ISW	1	—	—	Matsumoto (1959)	
	02°00'S	98°59'E		2	—	—	Matsumoto (1959)	
	02°07'S	99°53'E		1	—	—	Matsumoto (1959)	
	01°29'S	100°07'E		2	—	—	Matsumoto (1959)	
	01°29'S	100°07'E	ISW	10	—	—	Matsumoto (1959)	
	00°52'S	99°25'E		1	—	—	Matsumoto (1959)	
	00°52'S	99°25'E		11	—	—	Matsumoto (1959)	
	00°52'S	99°25'E		7	—	—	Matsumoto (1959)	
	02°57'S	99°36'E	ISW	1	—	—	Matsumoto (1959)	
	03°12'S	99°26'E	ISW	1	—	—	Matsumoto (1959)	
Oct. 1929	01°45'N	71°05'E	ISW	1	—	7.08	Jones and Kumaran (1963)	Length not defined
	00°35'N	66°09'E	ISW	1	—	—	Jones and Kumaran (1963)	Length not defined
	03°45'S	56°33'E	ISW	2	—	6.05, 7.14	Jones and Kumaran (1963)	Length not defined
	05°01'S	54°46'E	ISW	1	—	5.94	Jones and Kumaran (1963)	Length not defined
	08°27'S	50°54'E	ISW	1	—	5.59	Jones and Kumaran (1963)	Length not defined
	11°55'S	49°55'E	ISW	2	—	4.7	Jones and Kumaran (1963)	Length not defined
	12°09'S	49°34'E	ISW	8	—	6.62-12.72	Jones and Kumaran (1963)	Length not defined
	09°10'S	45°17'E	ISW	1	—	6.58	Jones and Kumaran (1963)	Length not defined
	08°24'S	42°54'E	ISW	3	—	5.14-7.94	Jones and Kumaran (1963)	Length not defined
	07°24'S	41°51'E	ISW	56	—	4.68-8.75	Jones and Kumaran (1963)	Length not defined
Jan. 1930	04°45'S	40°10'E	ISW	15	—	5.42-12.16	Jones and Kumaran (1963)	Length not defined
	03°26'S	42°58'E	ISW	34	—	4.74-8.69	Jones and Kumaran (1963)	Length not defined
	04°21'S	42°56'E	ISW	2	—	6.11	Jones and Kumaran (1963)	Length not defined
	14°16'S	41°48'E	ISW	3	—	6.79	Jones and Kumaran (1963)	Length not defined
	16°12'S	42°04'E	ISW	14	—	4.79-9.14	Jones and Kumaran (1963)	Length not defined
	18°30'S	42°18'E	ISW	1	—	—	Jones and Kumaran (1963)	Length not defined
	21°13'S	42°26'E	ISW	3	—	5.69-5.88	Jones and Kumaran (1963)	Length not defined
	23°11'S	42°54'E	ISW	2	—	7.08-8.39	Jones and Kumaran (1963)	Length not defined
	25°14'S	36°21'E	ISW	29	—	4.62-7.42	Jones and Kumaran (1963)	Length not defined
	Manado, Celebes, Netherlands, East Indies		ISEW	—	1	115	Wade (1950a)	Fork length

Table 9.— Continued.

Date	Locality		Marine area code [see Rosa (1965)]	Number		Length (mm)	Reference	Remarks
	Lat.	Long.		Larvae	Juveniles			
Apr. 1948	Batangas, Luzon, Philippines		ISEW	—	7	143-178	Wade (1950a)	Fork length
May 1948	7°02'N 124°12'E		ISEW	—	2	33.5, 35	Wade (1950a)	Fork length
	Taal, Batangas Province, Luzon, Philippines		ISEW	—	4	127-175	Wade (1950a)	Fork length
	Batangas, Luzon, Philippines		ISEW	—	2	40, 44	Wade (1950a)	Fork length
Mar. 1949	Batangas, Luzon, Philippines		—	—	2	40, 68.4	Wade (1950a)	Fork length
	Batangas, Luzon, Philippines		—	—	1	80	Wade (1950a)	Fork length
Apr. 1949	Batangas, Luzon, Philippines		—	—	1	76.5	Wade (1950a)	Fork length
	Batangas, Luzon, Philippines		—	—	18	73-112	Wade (1950a)	Fork length
	Batangas, Luzon, Philippines		—	—	2	117.5-131	Wade (1950a)	Fork length
Aug.-Oct. 1950	Off southern Kyushu, Japan		ISEW	—	Numerous	150-250	Yabe et al. (1953)	Fork length
Sept. 1956	Calicut, India		ISW	—	6	72.0-140.0	Jones (1960)	Length given by Jones is standard length. Jones reported cap- ture of larger juve- niles not included here.
Oct. 1956	Vizhingam, India		ISW	—	1	116.5	Jones (1960)	
Nov. 1956	Vizhingam, India		—	—	1	162.0	Jones (1960)	
Jan. 1957	Vizhingam, India		—	—	8	34.3-75.0	Jones (1960)	
May 1958	Vizhingam, India		—	—	2	24.5, 40.6	Jones (1960)	
June 1958	Vizhingam, India		—	—	1	96.0	Jones (1960)	
Aug. 1956	00°01'S 133°02'W		ISEW	—	1	—	Strasburg (1960)	
	12°31'S 132°04'W		ISEW	—	2	—	Strasburg (1960)	
Jan. 1957	07°55'S 110°02'W		ISEW	—	1	—	Strasburg (1960)	
Feb. 1957	02°58'S 129°55'W		ISEW	—	1	—	Strasburg (1960)	
	14°57'S 146°20'W		ISEW	—	2	—	Strasburg (1960)	
Mar. 1957	08°12'S 145°12'W		ISEW	1	—	—	Strasburg (1960)	
June 1957	21°11'N 158°17.5'W		ISEW	1	—	—	Strasburg (1960)	
	21°25'N 157°21'W		ISEW	1	—	—	Strasburg (1960)	
	21°24.5'N 159°00'W		ISEW	1	—	—	Strasburg (1960)	
Dec. 1957	09°34'S 139°50'W		ISEW	2	—	—	Nakamura and Matsumoto (1967)	
Oct. 1960	12°29'N 43°03'E		ISEW	215	—	—	Parin (1967)	
July-Aug. 1960-61	Gulf of Tonkin		ISEW	22	—	3.5-6.0	Gorbulnova (1965a)	Length not defined
July-Sept. 1967	Hawaii		ISEW	—	25	—	Higgins (1970)	
July-Sept. 1968-71	21°30'-24°45'N 119°28'-121°30'E 03°30'-12°00'N 102°45'-115°15'E		ISEW	24	—	—	Chen and Tan (1973)	

Fig. 8). Larvae and juveniles have been reported from Hawaii (Strasburg 1960; Higgins 1970), near the Marquesas and Tuamotus and surrounding areas (Strasburg 1960; Nakamura and Matsumoto 1967), in the Gulf of Tonkin (Gorbulnova 1965a), in the Gulf of Aden (Gorbulnova 1965b; Parin 1967), around Taiwan and adjacent waters (Matsumoto 1959; Chen and Tan 1973), and off the coast of southern Japan (Yabe et al. 1953). These records suggest that *E. affinis* probably spawns throughout its range.

Euthynnus alletteratus

Based on the records of occurrence of postlarval and juvenile *E. alletteratus*, Padoa (1956) indicated that spawning in the Mediterranean occurred in the spring-time and in the summer. The summer spawning con-

clusion was based on postlarval material reported on by Ehrenbaum (1924); however, Matsumoto (1959) indicated that the identification of *E. alletteratus* by Ehrenbaum was erroneous. On the other hand, Belloc (1955) noted that spawning takes place in different parts of the Mediterranean chiefly in July-August. Ben-Tuvia (1957) indicated that young *E. alletteratus* 8 to 16 cm long are taken by "light fishing" from June to September along the Mediterranean coast of Israel, which, according to him, suggested summer spawning. Postel (1964) also indicated that the spawning season for *E. alletteratus* in the Mediterranean is in the summer (June-July-August).

In the eastern Atlantic, Postel (1950) noted that the spawning season was from April to November, including a peak from June to September along the coast of Dakar, Senegal. Further south along the coast of western Africa, Marchal (1963) indicated that peak spawning took place

in October and November. Along the Ivory Coast, Marchal (1963) indicated that the spawning season is very extended, at least from October to June. He noted an interruption of spawning during July to September coinciding with a cooling of the sea in the Ivory Coast area. Of interest is the series of larval tuna surveys conducted in the northwestern Gulf of Guinea in 1964 and 1965 by the Miami Laboratory, NMFS (National Marine Fisheries Service) (Richards et al. 1969a, 1969b, 1970). The cruises were made in the winter-spring "warm season" in the Gulf of Guinea (February-April 1964 and March-April 1965) and in the summer-fall "cool season" (August-October 1964). Larval *E. alletteratus* were caught during the cool season as well as the warm season (Table 10). Although the surveys did not cover all the months of the year, the results, together with observations made by Marchal (1963), suggest year-round spawning in the northwestern Gulf of Guinea. Around São Tomé and Príncipe the spawning season extends from October to December (Frade and Postel 1955; da Costa and Frade 1958).

The development of *E. alletteratus* gonads indicates an extended spawning season beginning in March and continuing to about November off the coast of Florida (de Sylva and Rathjen 1961). Potthoff and Richards

(1970) also concluded that *E. alletteratus* spawns over a long period in Florida waters. They based their conclusion on the occurrence of juveniles in the regurgitated food of seabirds in the Dry Tortugas, Fla.

Klawe and Shimada (1959) reported the capture of juvenile *E. alletteratus* during the months of March, April, June, July, and August in the Gulf of Mexico (Table 11) and suggested reproductive activity at least during these months if not also in other months of the year. The records of other larval and juvenile *E. alletteratus* shown in Table 11 suggest spawning in those areas also.

Marchal (1963) concluded that in the Mediterranean and along the west coast of Africa, *E. alletteratus* spawns during periods of the year when the water is warmest and that this species apparently reproduces throughout its range.

Euthynnus lineatus

Klawe (1963) found that *E. lineatus* spawning in the northern part of its distribution is limited to the summer months. He also noted that farther south, *E. lineatus* spawns throughout the year including a possible peak in early spring (Table 12).

Table 10.—Records of larval *Euthynnus alletteratus* in the northwestern Gulf of Guinea and off Sierra Leone (ASE¹). (From Richards et al. 1969a, 1969b, 1970.)

Date	Locality		No. of larvae	Date	Locality		No. of larvae
	Lat.	Long.			Lat.	Long.	
February 1964	04°20'N	08°09'W	78	October 1964	04°23'N	01°04'E	3
	04°51'N	05°30'W	1		02°53'N	01°02'W	1
	05°02'N	03°53'W	2		03°38'N	02°00'W	1
	04°15'N	01°32'W	1		04°00'N	02°38'W	4
	02°45'N	01°30'W	4	February 1965	04°09'N	03°10'W	5
	02°51'N	01°25'W	1		07°57'N	16°53'W	1
	04°20'N	01°30'W	1		06°29'N	16°28'W	5
	04°30'N	00°54'W	5		06°15'N	16°29'W	1
	04°34'N	00°49'W	1		09°00'N	16°02'W	1
	05°31'N	00°10'E	2		06°11'N	15°30'W	1
	05°28'N	00°10'E	2	February 1965	07°30'N	15°00'W	2
	04°48'N	00°01'E	4		08°30'N	15°27'W	1
	04°59'N	01°00'E	15		08°14'N	15°00'W	7
	04°30'N	01°30'E	3		07°26'N	15°01'W	1
March 1964	04°31'N	01°55'E	2		07°00'N	14°29'W	1
	05°01'N	03°58'W	1	March 1965	07°01'N	14°28'W	1
April 1964	04°32'N	05°01'W	5		07°08'N	13°30'W	1
	04°56'N	01°11'W	11		07°03'N	13°06'W	1
	04°54'N	00°30'W	33		06°49'N	13°04'W	4
	04°15'N	00°33'W	1		04°35'N	02°32'W	3
	03°52'N	01°03'W	1		04°06'N	02°33'W	1
	02°55'N	02°04'W	10		04°20'N	01°59'W	1
August 1964	03°31'N	02°04'W	10		04°08'N	01°28'W	1
	04°20'N	06°59'W	2		04°10'N	00°29'W	1
	04°32'N	06°19'W	1		04°22'N	00°06'W	9
	05°00'N	04°30'W	1		05°35'N	00°32'E	3
	04°21'N	02°02'W	1		05°05'N	00°25'E	1
	04°18'N	01°09'W	1		05°59'N	01°30'E	2
	04°27'N	01°44'W	8		05°45'N	01°30'E	1
	06°00'N	01°39'E	1		05°53'N	01°58'E	1
	06°09'N	02°37'E	1		04°15'N	02°30'E	2
September 1964	02°30'N	07°57'W	1				
	03°50'N	06°41'W	5				

¹Marine area code. See Rosa (1965).

Table 11.—Records of larval and juvenile *Euthynnus alletteratus* in the Atlantic and Mediterranean.

Date	Locality		Marine area code [see Rosa (1965)]	Number		Length (mm)	Reference	Remarks	
	Lat.	Long.		Larvae	Juveniles				
June 1920	18°00'N	64°14'W	ASW	1	—	—	Matsumoto (1959)		
July 1920	33°07'N	77°00'W	ASW	4	—	—	Matsumoto (1959)		
	33°07'N	77°00'W		5	—	—	Matsumoto (1959)		
May 1921	17°55'N	64°48'W	ASW	1	—	—	Matsumoto (1959)		
Nov. 1921	07°22'N	46°51'W	ASW	1	—	—	Matsumoto (1959)		
	05°35'N	51°08'W	ASW	1	—	—	Matsumoto (1959)		
	05°35'N	51°08'W		2	—	—	Matsumoto (1959)		
	05°35'N	51°08'W		10	—	—	Matsumoto (1959)		
	05°06'N	51°35'W	ASW	1	—	—	Matsumoto (1959)		
	05°06'N	51°35'W		14	—	—	Matsumoto (1959)		
	05°06'N	51°35'W		2	—	—	Matsumoto (1959)		
	35°42'N	73°43'W	ASW	5(?)	—	—	Matsumoto (1959)		
June 1953	25°35'N	79°25'W	ASW	—	1	8.8	Klawe (1960)	(¹)	
July 1954	34°35'N	75°15'W	ASW	—	2	25, 35	Klawe (1961)	(¹)From stomach of <i>Euthynnus</i>	
Aug. 1954	28°59'N	88°07'W	ASW	—	4	27-41	Klawe and Shimada (1959)	(¹)	
	28°36'N	87°58'W	ASW	—	4	28-33	Klawe and Shimada (1959)	(¹)	
	29°05'N	88°10'W	ASW	—	86	21-44	Klawe and Shimada (1959)	(¹)	
	27°34'N	89°00'W	ASW	—	3	26-38	Klawe and Shimada (1959)	(¹)	
	27°58'N	88°03'W	ASW	—	2	76-80	Klawe and Shimada (1959)	(¹)	
	29°28'N	87°30'W	ASW	—	38	11-47	Klawe and Shimada (1959)	(¹)	
	28°59'N	88°02'W	ASW	—	4	56-108	Klawe and Shimada (1959)	(¹)	
	28°46'N	88°40'W	ASW	—	5	24-36	Klawe and Shimada (1959)	(¹)	
June 1955	29°12'N	88°34'W	ASW	—	29	22-174	Klawe and Shimada (1959)	(¹)	
	28°40'N	88°58'W	ASW	—	10	21-31	Klawe and Shimada (1959)	(¹)	
Aug. 1955	28°50'N	87°50'W	ASW	—	4	3.5-5.3	Klawe and Shimada (1959)	(¹)	
	28°50'N	87°48'W	ASW	—	88	30-53	Klawe and Shimada (1959)	(¹)	
	28°47'N	87°57'W	ASW	—	16	31-55	Klawe and Shimada (1959)	(¹)	
	28°45'N	87°56'W	ASW	—	4	6.2-8	Klawe and Shimada (1959)	(¹)	
	28°55'N	88°00'W	ASW	—	90	29-65	Klawe and Shimada (1959)	(¹)	
	28°55'N	87°57'W	ASW	—	116	4-80	Klawe and Shimada (1959)	(¹)	
	29°01'N	87°48'W	ASW	—	60	17-68	Klawe and Shimada (1959)	(¹)	
	28°12'N	88°43'W	ASW	—	11	49-86	Klawe and Shimada (1959)	(¹)	
	28°17'N	88°37'W	ASW	—	12	32-94	Klawe and Shimada (1959)	(¹)	
	Sept. 1955	29°27'N	86°55'W	ASW	—	52	24-49	Klawe and Shimada (1959)	(¹)
	—	Gulf of Mexico	ASW	—	8	19-29	Klawe and Shimada (1959)	(¹)	
	Aug. 1956	28°50'N	87°50'W	ASW	—	33	21-82	Klawe and Shimada (1959)	(¹)
Oct. 1957	Off Takoradi, Ghana	ASE	{ Single specimen Up to 60 specimens per catch }	—	—	Kazanova (1962)	Length not defined		
Dec. 1958									
July 1960	Off Dakar, Senegal	ASE		—	4.14-6.10	Kazanova (1962)	Length not defined		
Aug.-Sept. 1964	Around Cuba	ASW	20	—	3.0-5.4	Gorbunova and Salabarrí (1967)	Length not defined		
Feb.-Mar. 1963		06°18'N	23°20'W	ASE	2	3.8, 3.7	Zharov and Zhudova (1969)	Length not defined	
		04°40'N	24°28'W	ASE	1	4.4	Zharov and Zhudova (1969)	Length not defined	
		10°00'S	34°33'W	ASW	1	8.7	Zharov and Zhudova (1969)	Length not defined	
		03°00'N	30°00'W	ASW	1	4.2	Zharov and Zhudova (1969)	Length not defined	
	03°37'S	30°04'W	ASW	1	4.4	Zharov and Zhudova (1969)	Length not defined		
Apr.-July 1960-67	24°30'N	82°50'W	ASW	—	47	29-135	Potthoff and Richards (1970)	Standard length	
Oct. 1964	07°S	12°E	ASE	4	—	4.2-10.2	Zhudova (1969a)	Approximate locations Length not defined	
Dec. 1966	05°N	04°30'W							
Feb. 1966	04°30'N	04°30'W							
Aug.-Oct. 1964	09°20'N	19°41'W	ASE	No numbers given	—	—	Zhudova (1969b)		
Throughout the year	Ivory Coast and Ghana		ASE	—	Numerous	—	Marchal (1963)		
June-Aug. 1959	Haifa Bay		ASE	—	Numerous	80-240	Ben-Tuvia (1957)	Length not defined	
Aug.-Oct. 1959	Dardanelles		ASE	—	Numerous	145-220	Demir (1963)	Fork length	
Aug.-Sept. 1959	Sea of Marmara		ASE	—	Numerous	180-250	Demir (1963)	Fork length	

¹Total length measured from tip of snout to shortest median ray of caudal fin.

Table 12.—Average numbers of *Euthynnus lineatus* larvae caught per hour of surface plankton tow off Cape Blanco, Costa Rica. (From Klawe 1963:465.)

Month	No. of larvae	Month	No. of larvae
January	1.5	July	0.1
February	0.1	August	0.2
March	3.2	September	1.4
April	14.9	October	0.0
May	0.6	November	0.2
June	0.0	December	0.7

Records of larval and juvenile *E. lineatus* from the eastern Pacific and from near Costa Rica are shown in Tables 13 and 14, respectively. The records indicate the probable spawning periods and localities in the eastern tropical Pacific Ocean.

3.17 Spawn

There is very little information on the fertilized eggs of *Euthynnus* in the literature. Delsman (1931) described the eggs of *Thynnus thunnina* (= *E. affinis*) which he had earlier identified as eggs of *Scomber* (= *Rastrelli*-

Table 13.—Records of larval and juvenile *Euthynnus lineatus* in the eastern tropical Pacific Ocean (ISE¹). The lengths of the specimens were given as total or fork length in the various references listed in the table; however, both were taken in the same manner, i.e., from the tip of the snout to the shortest median ray in the caudal fin.

Date	Locality		Number		Total or fork length (mm)	Collector or reference
	Lat.	Long.	Larvae	Juveniles		
Jan. 1922	06°49'N	80°25'W	4	1	—	Matsumoto (1959)
	06°49'N	80°25'W	1	—	—	Matsumoto (1959)
	06°49'N	80°25'W	1	—	—	Matsumoto (1959)
	06°49'N	80°25'W	13	—	—	Matsumoto (1959)
	06°40'N	80°47'W	4	—	—	Matsumoto (1959)
	06°40'N	80°47'W	1	—	—	Matsumoto (1959)
	06°40'N	80°47'W	1	—	—	Matsumoto (1959)
	06°40'N	80°47'W	2	—	—	Matsumoto (1959)
	06°40'N	80°47'W	2	—	—	Matsumoto (1959)
	06°40'N	80°47'W	58	—	—	Matsumoto (1959)
	06°48'N	80°33'W	1	—	—	Matsumoto (1959)
	06°48'N	80°33'W	2	—	—	Matsumoto (1959)
	06°48'N	80°33'W	2	—	—	Matsumoto (1959)
	06°48'N	80°33'W	1	—	—	Matsumoto (1959)
	06°48'N	80°33'W	1	—	—	Matsumoto (1959)
	08°24'N	79°23'W	13	—	—	Matsumoto (1959)
	08°40'N	79°23'W	25	—	—	Matsumoto (1959)
Sept. 1928	07°06'N	79°55'W	2	—	—	Matsumoto (1959)
	07°16'N	78°30'W	1	—	—	Matsumoto (1959)
Mar. 1947	07°55'N	79°02'W	1	—	—	Matsumoto (1959)
	08°20'N	84°10'W	—	8	48-86	Schaefer and Marr (1948)
	09°20'N	85°20'W	—	10	29-56	Schaefer and Marr (1948)
	09°10'N	85°20'W	—	1	61	Schaefer and Marr (1948)
May 1949	10°58'N	89°56'W	—	2	7.5, 10.5	Mead (1951)
	11°20'N	87°20'W	—	23	14-18	Mead (1951)
	12°50'N	89°40'W	—	2	18, 24	Mead (1951)
Oct. 1951	24°35'N	112°05'W	—	1	9.7	Sefton, Jr. ²
Jan. 1955	12°34'N	89°50'W	—	8	25 (mean)	Clemens (1956)
	08°43'N	84°11'W	—	34	17-38	Clemens (1956)
Nov. 1955	07°42'N	79°20'W	—	1	30	Eastropac Expedition ²
	03°01'N	82°15'W	—	6	27-38	Eastropac Expedition ²
Dec. 1955	11°48'N	88°25'W	—	1	46	Eastropac Expedition ²
Nov. 1955	08°31.3'N	79°32'W	2	—	—	Klawe (1963)
Aug. 1956	26°04.5'N	112°48'W	1	—	7.0	La Jolla Lab., NMFS ²
Sept. 1956	15°05'N	93°54'W	—	3	15-27	Klawe (1963)
Oct. 1956	12°51'N	93°05'W	—	1	51	Klawe (1963)
Nov. 1956	14°00'N	96°11'W	—	1	30	Schaefer and Shimada ²
Feb. 1957	17°24'N	102°04'W	—	1	21	Renner and Hark ²
Aug. 1957	29°12'N	115°39'W	—	1	—	La Jolla Lab., NMFS ²
	31°11'N	114°15'W	—	2	29.5, 353	La Jolla Lab., NMFS ²
	05°34'N	81°29'W	—	1	60	Klawe (1963)
May 1958	08°28'N	84°21'W	1	—	—	Klawe (1963)
	15°15'N	95°23'W	11	—	—	Klawe (1963)
	18°44'N	104°21'W	—	5	20-27	Klawe (1963)
	17°49'N	103°38.5'W	—	99	7.5-45	Klawe (1963)
	21°36'N	106°44'W	—	3	18-48	Klawe (1963)
	16°39'N	100°05'W	1	—	—	Klawe (1963)
	17°24'N	101°25'W	6	—	—	Klawe (1963)
	18°44'N	104°21'W	1	—	—	Klawe (1963)

Table 13.—Continued.

Date	Locality		Number		Total or fork length (mm)	Collector or reference
	Lat.	Long.	Larvae	Juveniles		
Nov. 1958	14°56.5'N	93°06.5'W	11	—	—	Klawe (1963)
	15°39'N	93°59.5'W	1	—	—	Klawe (1963)
	14°18'N	95°02.8'W	1	—	—	Klawe (1963)
	15°02'N	95°07.5'W	1	—	—	Klawe (1963)
	14°21'N	97°01'W	3	—	—	Klawe (1963)
	14°21'N	97°01'W	24	—	—	Klawe (1963)
	15°31'N	97°44'W	5	—	—	Klawe (1963)
Dec. 1958	15°31'N	97°44'W	15	—	—	Klawe (1963)
	15°36'N	99°23.5'W	1	—	—	Klawe (1963)
Jan. 1959	15°29.5'N	98°32.5'W	4	—	—	Klawe (1963)
	15°29.5'N	98°32.5'W	4	—	—	Klawe (1963)
Feb. 1959	19°46'N	105°44'W	5	—	—	Klawe (1963)
Apr. 1959	08°12'N	83°15.5'W	—	6	12-18	Broadhead and Chatwin ²
	08°12'N	83°17'W	—	1	7.5	Broadhead and Chatwin ²
	08°15'N	83°23'W	—	6	13-28	Broadhead and Chatwin ²
Sept. 1959	15°39'N	97°00'W	2	—	—	Klawe (1963)
	14°20'N	95°59'W	6	—	—	Klawe (1963)
	14°20'N	95°59'W	6	—	—	Klawe (1963)
	14°54.8'N	95°07.1'W	36	—	—	Klawe (1963)
	14°21.5'N	94°01'W	5	—	—	Klawe (1963)
	16°28'N	99°32.5'W	2	—	—	Klawe (1963)
Feb. 1961	12°35'N	93°40'W	—	3	7.5-9.5	Vann ²
Oct. 1966	Entrance, Gulf of California		2	—	—	Klawe et al. (1970)
Nov. 1966	Entrance, Gulf of California		3	—	—	Klawe et al. (1970)
Dec. 1966	Off Tres Marias Is.		1	—	—	Klawe et al. (1970)
	Entrance, Gulf of California		1	—	—	Klawe et al. (1970)

¹Marine area code. See Rosa (1965).²As reported in Klawe (1963).

ger) *kanagurta*. Delsman noted that the egg diameters were 0.85 to 0.95 mm and that the diameter of the oil globule ranged from 0.21 to 0.24 mm. Sanzo (1932) described some fertilized eggs which he tentatively identified as belonging to *Euthynnus alletteratus*. The eggs were buoyant, spherical, and transparent, and were about 1.08 mm in diameter with an oil globule 0.28 mm in diameter. The dimensions of the fertilized eggs were very similar to that of *Auxis* and *Thunnus* eggs, but the embryos did not show yellow pigmentation as in those species. The yolk sac was rich in black pigment.

Houde and Richards (1969) reported on the collection of some fertilized eggs which were later determined to be from *E. alletteratus*. The eggs were collected from May through August 1969 in the Straits of Florida off Miami and returned to the laboratory for incubation. In a successful attempt at hatching some of the fertilized eggs, examination of the resulting larvae reared to 12 days past hatching revealed that the larvae were those of *E. alletteratus*. They noted that the larvae hatched within 12 h of collection and probably within 24 h after the eggs were fertilized. They did not include a description of the fertilized eggs.

Calkins and Klawe (1963) stated that the fertilized eggs of *E. lineatus* are pelagic but they had never been specifically identified in plankton collections.

3.2 Preadult phase

3.21 Embryonic phase

Euthynnus affinis

Delsman (1926), as stated earlier, described some fertilized eggs of *Scomber* (= *Rastrelliger*) *kanagurta* which he later reidentified as *Thynnus thunnina* (= *E. affinis*). He noted that the eggs took less than 24 h to hatch. Delsman's drawing of a newly hatched larva indicates a size of approximately 2.1 mm at hatching. He counted a total of 39-41 "myotomes" in larvae of various stages of development (Fig. 11). Whether these were actually larvae of *E. affinis* has not been verified.

Euthynnus alletteratus

Houde and Richards (1969) collected the fertilized eggs of *E. alletteratus* and were successful in hatching the eggs and rearing the larvae up to 18 days past hatching. The larvae were slightly less than 3 mm long at hatching. The newly hatched larvae had a large yolk sac that contained a single prominent oil globule, the eyes were unpigmented, and the mouth and gut were not functional. The yolk was absorbed, the eyes became pigmented, and

Table 14.—Larval and juvenile *Euthynnus lineatus* captured off Cape Blanco, Costa Rica (ISE¹). (From Klawe 1963, table 5.)

Date	Location from Cape Blanco	Number		Total length (mm)
		Larvae	Juveniles	
Nov. 1958	20 mi S	1	—	6.5
	20 mi S	1	—	9.0
	20 mi SSW	1	—	6.0
	20 mi SSW	2	—	5.0
Jan. 1959	20 mi S	—	8	21-39
	20 mi S	—	43	14-25
Feb. 1959	20 mi S	—	8	25-50
	20 mi S	1	—	5.0
Mar. 1959	20 mi S	3	—	5.1-6.7
	20 mi S	1	—	6.7
	5 mi SE	2	—	6.2-8.2
	5 mi SE	6	—	5.2-9.2
Apr. 1959	5 mi SE	1	—	5.3
	20 mi S	—	4	11-25
	5 mi SE	—	77	16-25
	20 mi S	2	—	6.5-7.7
	20 mi S	7	—	5.0-8.2
	20 mi SE	12	—	4.1-7.1
	5 mi SE	23	—	4.5-7.5
	5 mi SE	25	—	4.4-7.5
	5 mi SE	12	—	4.4-7.2
	5 mi SE	88	—	4.4-14.2
May 1959	10 mi SE	—	11	16-25
	10 mi SE	5	—	5.5-8.0
	10 mi SE	1	—	8.5
	10 mi SE	2	—	6.0-13.0
June 1959	10 mi W	—	2	ca.17
Aug. 1959	12 mi SE	3	—	4.6-8.8
	6 mi SE	—	3	15-17
Sept. 1959	20 mi S	4	—	4.8-5.7
	10 mi S	5	—	6.1-7.4
	10 mi S	4	—	5.0-7.3
	10 mi S	5	—	4.4-7.5
Nov. 1959	20 mi S	—	4	11.5-53
	20 mi S	1	—	4.4
Jan. 1960	10 mi S	9	—	4.1-5.5
	10 mi S	2	—	4.6-4.8
Feb. 1960	20 mi SSW	—	1	18
Mar. 1960	10 mi S	—	12	15-28
	20 mi S	6	—	3.3-6.3
	20 mi S	19	—	4.3-8.6
	10 mi S	6	—	3.7-6.7
May 1960	10 mi S	4	—	6.6-8.3
	20 mi S	—	14	13-21
	10 mi S	—	6	9.5-24
	10 mi S	1	—	6.5
July 1960	10 mi S	—	4	13-17
	10 mi S	—	62	10-24
	10 mi S	1	—	7.0
Aug. 1960	10 mi S	1	—	6.0
	20 mi S	—	1	19
	10 mi S	—	3	12-18
Sept. 1960	10 mi S	—	51	12.5-24
Oct. 1960	10 mi S	1	—	7.5

¹ Marine area code. See Rosa 1965.

the mouth and gut were functional within 48 h after hatching.

Euthynnus lineatus

No information.

3.22 Larvae and adolescent phases

The larvae and juveniles of all three species of *Euthynnus* have been described in detail (e.g., Schaefer and Marr 1948; Wade 1950a; Mead 1951; Matsumoto 1958, 1959; Jones 1960). The following descriptions of young *Euthynnus* are taken primarily from the above references.

Euthynnus affinis

The smallest specimen identified by Matsumoto (1958) as *E. affinis* measured 4.6 mm TL (Fig. 12a). The head length is moderate (33.9% TL), there are 40 myomeres, and the abdominal sac is nearly triangular. The mouth is fairly large (about 71.9% of the head length) and contains 12 teeth on the upper jaw and 9 teeth on the lower jaw. The distance from the tip of the snout to the anterior edge of the orbit is almost equal to the orbit diameter. Three long spines are present on the posterior edge of the preopercle; the longest spine is the one at the angle. Generally, a single chromatophore is found at the middle of the lower jaw and at the symphysis of the pectoral girdle.

The median fins show very little development; there are 4 or 5 rays in the caudal fin and only strong striations representing rays in the incipient anal and dorsal fins. The pelvic fins are undeveloped and the pectoral fins show only striations.

There are 13 and 15 teeth in the upper and lower jaws, respectively, and the preopercular spines have increased to 6 in a 5.5 mm TL specimen (Fig. 12b).

Five short spines are present in the first dorsal fin and about nine rays in the caudal; the other median fins and the pectorals still show only strong striations and the pelvic fins are just emerging as small buds.

The single chromatophore at the middle of the mandible and that at the pectoral symphysis are still evident.

A 7.6 mm TL specimen exhibits some striking changes, particularly in pigmentation. A series of four or five chromatophores is present on the anterior half of the mandible and the first dorsal fin is almost completely pigmented.

The head comprises 39.8% of the total length and the snout length is much greater than the diameter of the orbit. About 16 teeth are present on both the upper and lower jaws, and 7 spines are noticeable on the posterior edge of the preopercle.

There are 8 spines in the first dorsal fin; the length of the longest spine is less than half the distance between the dorsal fin insertions. The second dorsal and anal fin rays are further developed and, although the rays are not clearly evident, about 11 radials in the second dorsal and 12 in the anal are present. The first 7 dorsal and 6 anal finlet radials are also evident. There are 9 + 9 rays in the caudal fin and the pelvic fins are complete with 1 spine and 5 rays; about 5 rays are noticeable in the pectoral fins.

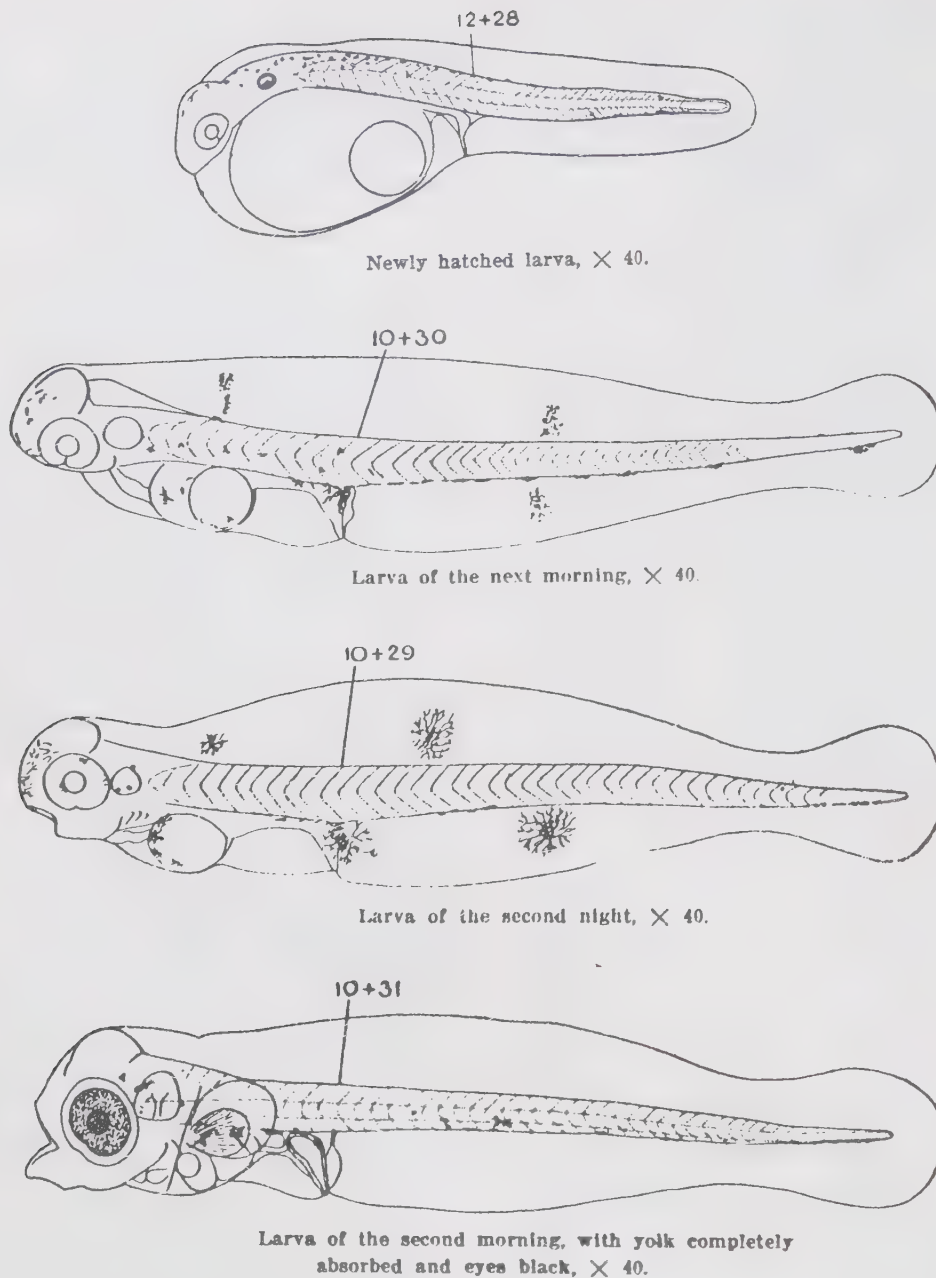


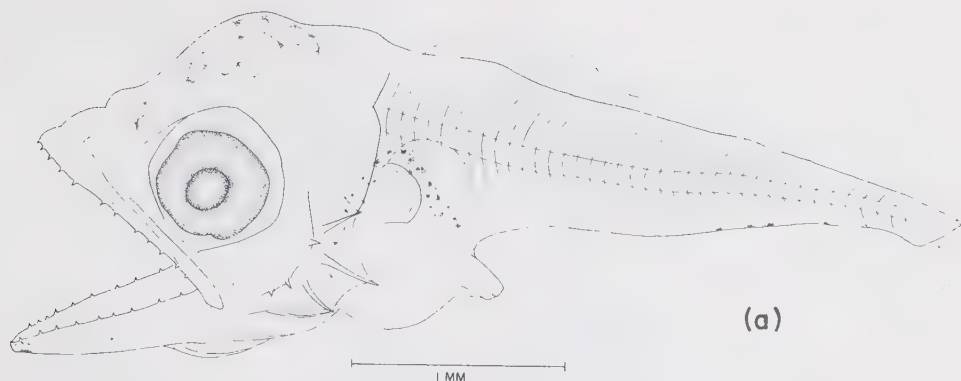
Figure 11.—Larvae of *Euthynnus affinis*. (From Delsman 1926, figs. 3-6.)

The first dorsal fin is heavily pigmented, and the pigmentation at the tip of the snout is more extensive in a 9.6 mm TL specimen (Fig. 12d). Chromatophores now extend over two-thirds of the length of the mandible and the chromatophore at the symphysis of the pectoral girdle still persists.

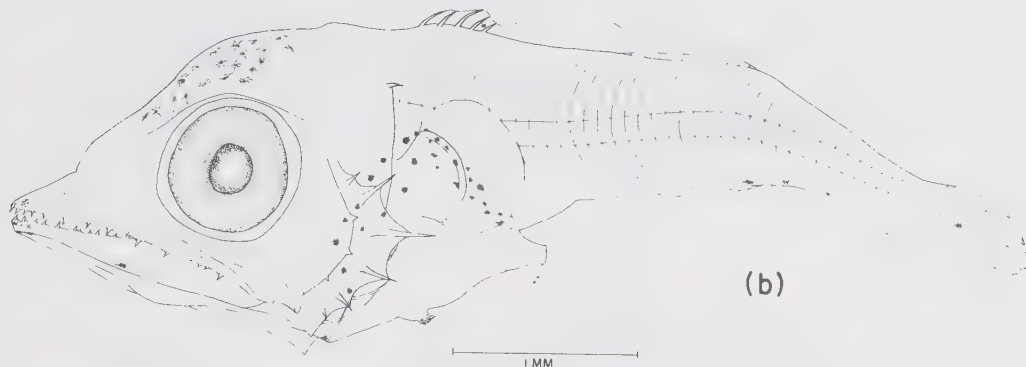
The first dorsal fin now has 13 spines and the length of the longest spine is greater than half the distance be-

tween the dorsal fin insertions. There are 13 rays in the second dorsal and anal fins.

Figure 12.—*Euthynnus affinis* larvae: (a) 4.6 mm; (b) 5.5 mm; (c) 7.6 mm; (d) 9.6 mm. (From Matsumoto 1958, figs. 15-17.) The body length, total or fork length, was measured from the tip of the snout to the fork of the tail when the tail was forked, and to the tip of the longest ray when the tail was not forked.



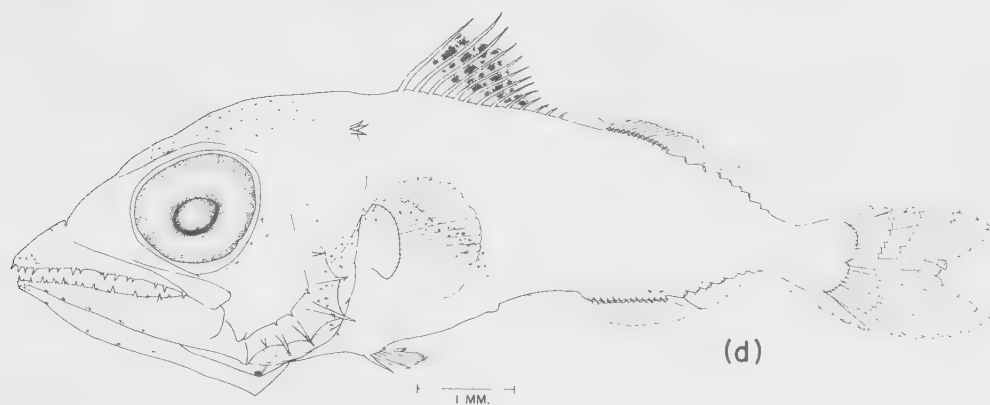
(a)



(b)



(c)



(d)

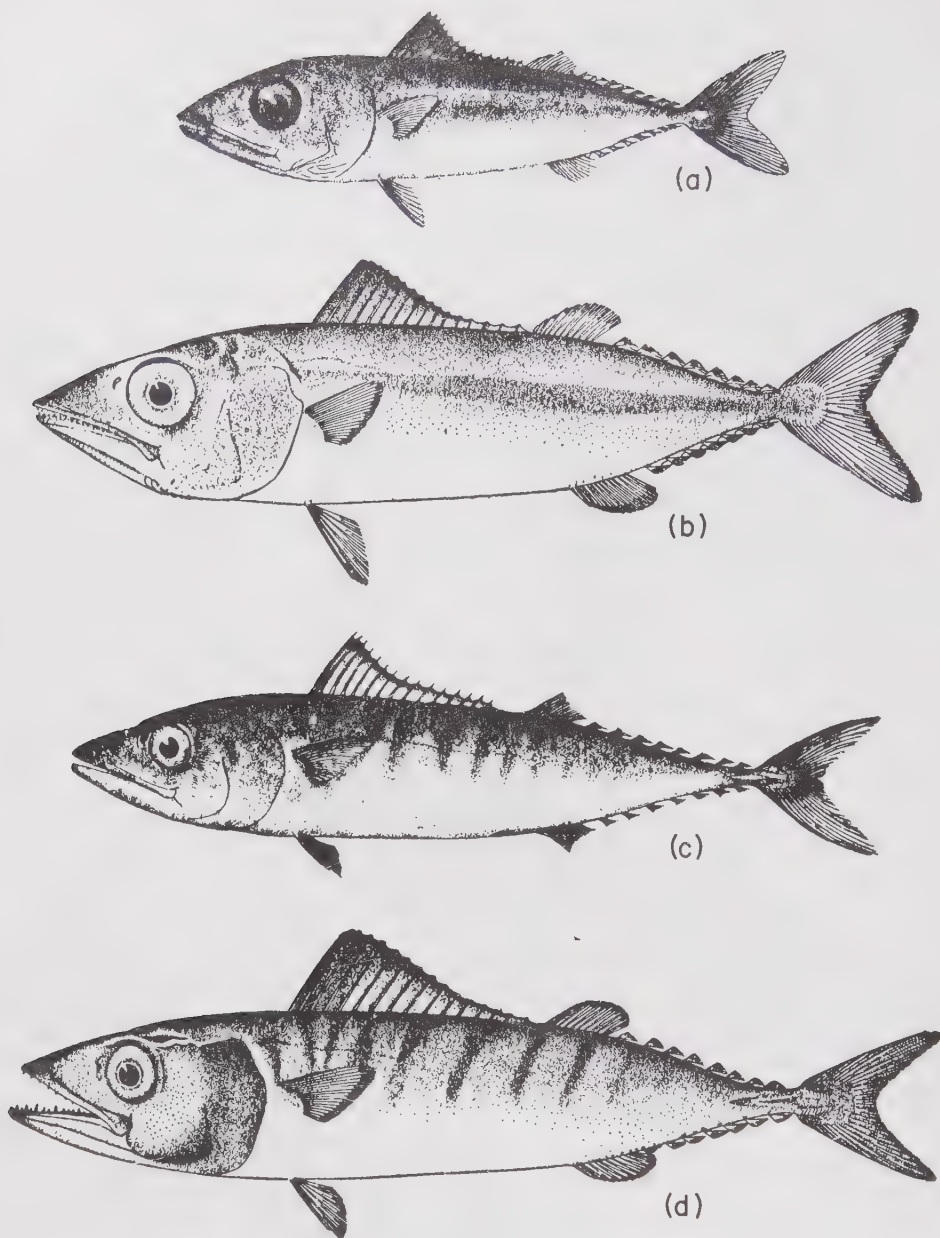


Figure 13.—Juvenile *Euthynnus affinis*: (a) 24.5 mm SL; (b) 33.5 mm FL; (c) 56.6 mm SL; (d) 67 mm FL; (e) 96.0 mm SL; (f) 110 mm FL; (g) 156 mm FL. (From Wade 1950a, figs. 10-13; Jones 1960, figs. 1-3.)

Wade (1950a) and Jones (1960) described juvenile *E. affinis* ranging in length from 24.5 mm SL (standard length) to 156 mm FL (Fig. 13). In the 24.5 mm SL specimen (Fig. 13a), all the larval characters are lost except for the vestiges of the preopercular spines (Jones 1960). The color of the body in the 24.5 mm SL and in the 33.5 mm FL (Fig. 13b) specimens is light brown dorsally and becomes paler toward the midline. A dark longitudinal

band is present along the lateral midline and ventrally the body is pale.

According to Wade (1950a) the color of the body and the head darkens as the fish grows larger and about 9 to 13 darker vertical bars begin to develop above the lateral midline on specimens about 60 mm FL.

The first dorsal has 16 spines and the posterior spine nearly reaches the base of the second dorsal. There are 12



to 14 rays (mostly 13) in the second dorsal and 13 or 14 rays in the anal fin. There are 8 dorsal and 7 anal finlets.

The gill raker count on a 35 mm FL specimen was $4 + 1 + 20$ and increased to $(7-8) + 1 + (22-23)$ in specimens of 127 to 175 mm FL (Wade 1950a).

Euthynnus alletteratus

See section 3.21.

In a 4.6 mm TL specimen of *E. alletteratus* (not figured), no visible indication of spine or ray development is evident in the unpaired fins. The future fins are represented by a continuous membrane which starts near the nape and extends around the caudal end to the anal

opening. There are 40 myomeres including the urostyle; the urostyle is incompletely developed and extends posteriorly in line with the longitudinal axis of the body.

Chromatophores are present at the pectoral girdle symphysis and immediately anterior to the anal opening along the midventral line. There are about 3 chromatophores over the forebrain and about 12 over the mid-brain and a row of 3 or 4 well-spaced chromatophores is evident over the middle two-thirds of the length of the lower jaw (Matsumoto 1959).

A 5.5 mm TL specimen (Fig. 14a) shows the development of four short spines in the first dorsal fin. The unpaired fins are beginning to develop, and the urostyle has turned upward. Chromatophores along the margin of the

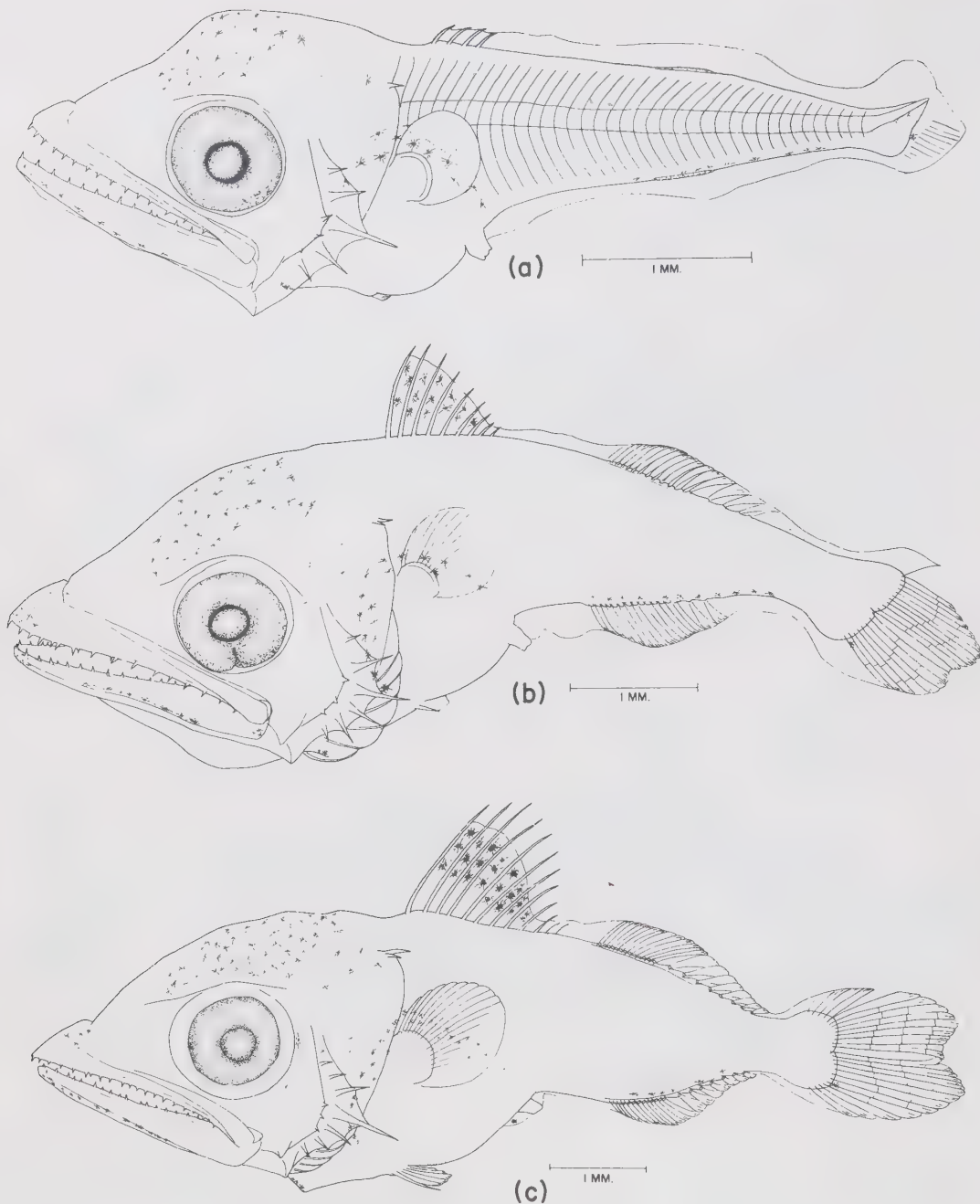


Figure 14.—*Euthynnus alletteratus* larvae: (a) 5.5 mm; (b) 7.5 mm; (c) 9.3 mm. (From Matsumoto 1959, figs. 8-10.) (See Fig. 12 for definition of body length.)

lower jaw have increased and cover the anterior two-thirds of the jaw length. Nine chromatophores are present on the midventral line from the anal fin origin to the caudal peduncle (Matsumoto 1959).

A 7.5 mm TL specimen (Fig. 14b) has 9 very long spines in the first dorsal fin. There are 12 or 13 rays in the second dorsal, 14 rays in the anal, and about 17 rays in the caudal fin.

Pigmentation is increased on the first dorsal fin and about 13 well-scattered chromatophores are present on the outer two-thirds of the fin between the first and seventh spines. The chromatophores along the lower jaw have increased and now appear closer together. The pigmentation along the midventral edge of the body consists of about 11 regularly spaced chromatophores although some specimens may have as many as 15 (Matsumoto 1959).

The most noticeable change in a 9.3 mm TL specimen (Fig. 14c) is the extremely long spines in the first dorsal fin. Similar to *E. lineatus* of comparable size, the length of the longest spine is about equal to the body depth measured at the origin of the second dorsal fin. The second dorsal and anal fins have 13 rays. The posterior edge of the caudal fin now shows signs of becoming forked and the ventral fins are beginning to enlarge. Pigmentation on the outer half of the first dorsal fin membrane has increased; there are 22 chromatophores extending over 8 interspinous membranes (Matsumoto 1959).

Matsumoto (1959) noted many changes in a 10.6 mm TL and a 11.5 mm TL specimen (not figured). Both specimens have completely developed dorsal and anal fins including 16 spines and 13 rays in the dorsal, followed by 8 finlets, and 14 rays in the anal followed by 7 finlets. The caudal fin is more clearly forked and the pelvic fins are longer. The 11.5 mm TL specimen has 20 + 19 vertebrae. An increase in pigmentation is evident in several places. The lower jaw bears two rows of chromatophores (the larger specimen has a third row) and the upper jaw has a single row of chromatophores along two-thirds of its length.

Matsumoto (1959) also described postlarval and juvenile *E. alletteratus* ranging in length from 12.0 to 58.0 mm TL (Fig. 15). The pigmentation along the dorsal and ventral edges of the body and along the midlateral line noted in the 10.6 and 11.5 mm TL specimens was also evident in the 12.0 mm TL specimen (Fig. 15a). Distinctive changes occurred between the 12.0 and 18.5 mm TL specimens (Fig. 15b). The abdominal sac was more elongate and the anus was more posteriorly placed in the larger specimen. The head parts, particularly the mouth, appeared smaller in relation to the total length and the fins and finlets were more clearly defined. The outline of the dorsal fin in the 26.0 mm TL specimen (Fig. 15c) resembles that of an adult and the body is narrower, relative to the total length than in the 18.5 mm TL specimen. For specimens larger than 26.0 mm TL the only noticeable change is in the increased pigmentation on the body. At about 40 mm TL one to three very faint spots or ventral bars appear along the dorsal third of the body. The number of bars increases to about 10 in a 58.0 mm TL specimen (Fig. 15d) and to 13 on a 94.3 mm TL fish (not figured).

Richards and Dove (1971) described in detail the internal development of young *E. alletteratus* ranging in standard length from 3.5 to 24.0 mm. Anatomical features of *E. alletteratus* were described and compared with those of *K. pelamis*, *Thunnus albacares*, *T. obesus*, *T. thynnus*, *T. alalunga*, *T. atlanticus*, and *Auxis* spp. The fol-

lowing anatomical features were examined: the sensory organs including the eyes, olfactory organs and acoustico-lateralis systems, the nervous system (brain), swim bladder, kidney, gonads, liver, pancreas, spleen, digestive system, cardiovascular system, gills, skeleton, musculature, and pigmentation. Potthoff and Richards (1970) also made observations on the development of the axial skeleton of *E. alletteratus* and also computed a regression equation to estimate the standard length of a specimen based on the length of the vertebral column. The equation is, $SL = 3.66 + 1.22 VL$, where SL is standard length in millimeters, and VL is vertebral column length in millimeters.

Euthynnus lineatus

The smallest larval *E. lineatus* identified by Matsumoto (1959) measured 5.0 mm TL (Fig. 16a). The head is relatively large (about 37% TL) and the mouth is also large and contains about eight teeth on each side of both jaws.

As in the other species of *Euthynnus* at the same stage, the abdominal sac is short and triangular, and the anus is located near the middle of the body. Spines and rays are undeveloped in all the fins. There are 38 or 39 myomeres including the urostyle.

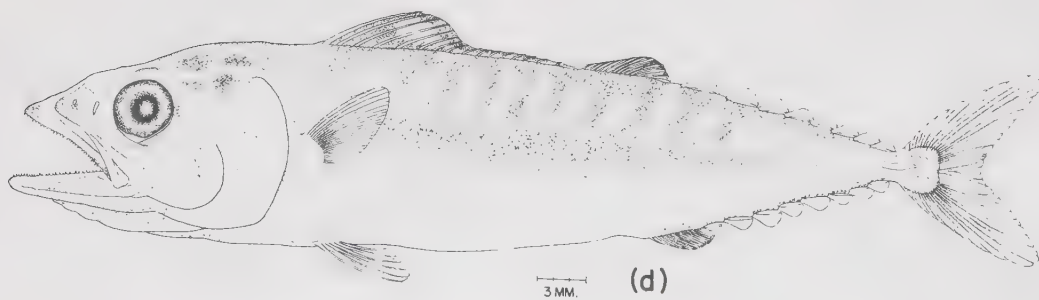
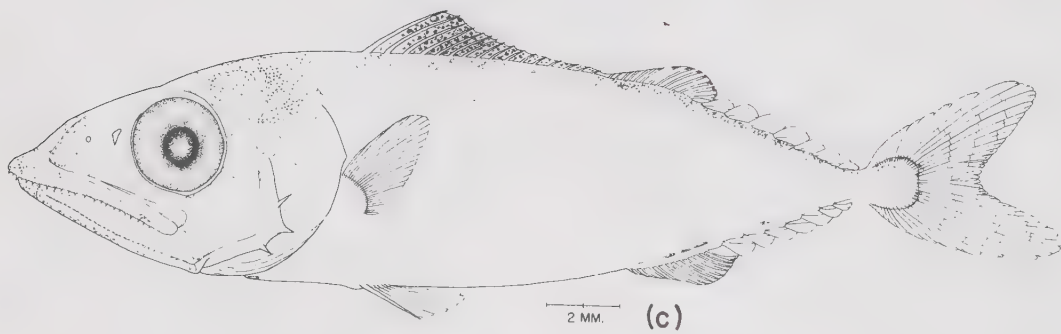
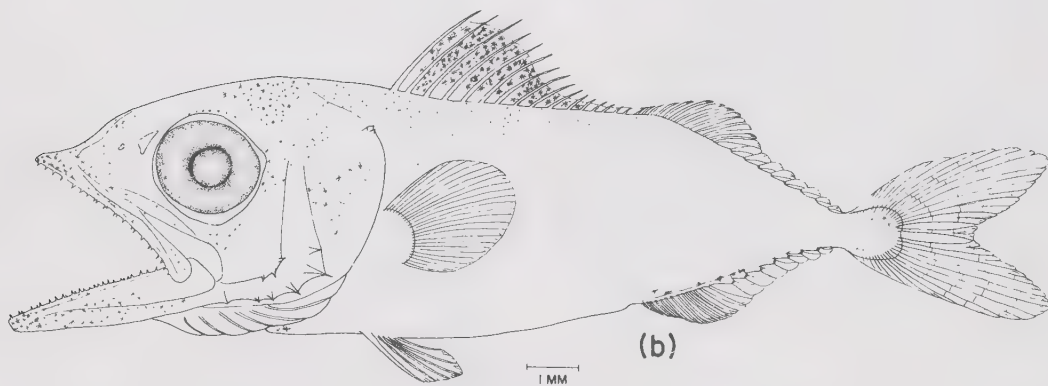
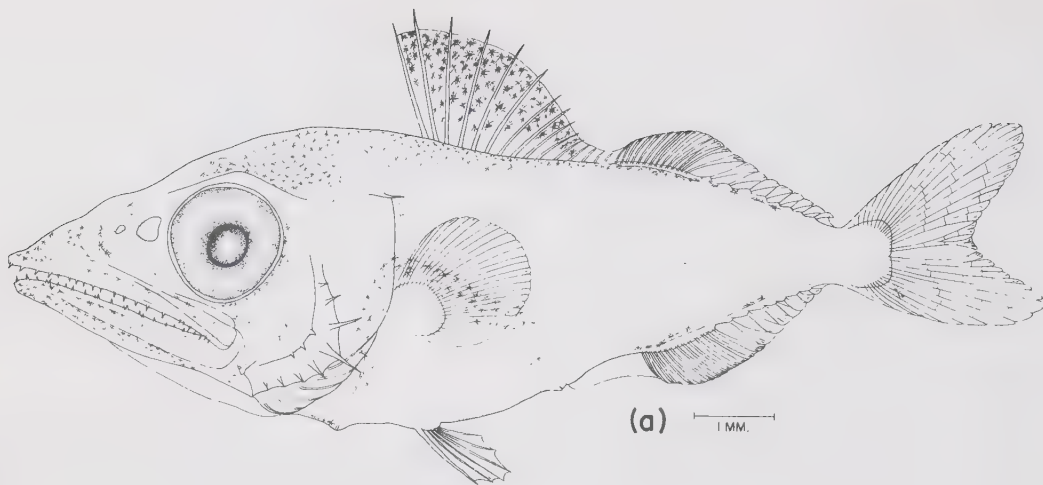
Chromatophores are present at the symphysis of the pectoral girdle and anterior to the anal opening. There is no pigment on the lower jaw at this stage of development (Matsumoto 1959).

There are 5 short spines in the region of the first dorsal fin and posterior to these, 2 more are beginning to develop in a 6.0 mm TL specimen (Fig. 16b). The second dorsal and anal fin rays are still poorly developed and are difficult to distinguish; there are 17 rays in the caudal fin. Three or four chromatophores can be seen near the middle of the lower jaw (Matsumoto 1959).

In a 7.1 mm TL specimen (Fig. 16c) the first dorsal fin has 7 definite spines, of which the 6 anterior ones are slightly greater in length. Three additional weak spines are beginning to develop but the fin rays are poorly formed. The caudal fin is beginning to fork and has 18 well-developed rays.

There are some striking changes in pigmentation in this specimen. The first dorsal fin between the second and sixth spines now has six large chromatophores. Chromatophores are present at the tips of the upper and lower jaws and seven more are found along the anterior two-thirds of the lower jaw (Matsumoto 1959).

Compared with the 7.1 mm TL specimen, a 9.3 mm TL specimen (Fig. 16d) has a well-developed dorsal fin. It has 12 well-developed spines of which the longest is about 78% of the body depth at the origin of the second dorsal fin. The second dorsal fin consists of 11 rays and the anal fin 12 rays. The pelvic fins are nearly complete in development and the pectorals have about 14 distinct rays. The first dorsal fin is pigmented over the first eight interspinous membranes; the pigmentation is generally concentrated on the outer two-thirds of the fin (Matsumoto 1959).



The abdominal sac is more elongate and the anal opening only slightly anterior to the anal fin origin in a 10.6 mm TL postlarval *E. lineatus* (Fig. 17a). The dorsal fin consists of 15 spines and 12 rays, and there are 8 dorsal finlets; the anal fin consists of 11 rays and there are 7 anal finlets (Matsumoto 1959).

The 18.6 mm TL juvenile (Fig. 17b) is already similar in body shape to larger juveniles due mostly to a gradual reduction in the head depth relative to body length and to the elongation of the abdominal sac, wherein the anal opening is closer to the anal fin origin.

The fins and finlets are more clearly defined in the 18.6 mm TL specimen. The dorsal fins have the full adult complement of 15 spines and 12 rays, followed by 8 finlets. The anal fin also has the full adult complement of 12 rays followed by 7 finlets. The caudal fin is well developed and more deeply forked, the pelvic fins are longer, and the pectorals have 24 completely formed rays which are comparable to the fully developed fins (24-26 rays) of the adults (Matsumoto 1959).

In the 21.0 mm TL specimen (Fig. 17c), except along the area of the lower jaw, the pigmented areas are more widespread (Matsumoto 1959).

3.3 Adult phase

3.31 Longevity

See sections 3.43 and 4.13.

The maximum size and longevity of *E. affinis* are not well defined. Kishinouye (1923) stated that *E. affinis* from Japanese waters grow to be 60 cm and 3.5 kg, and that on rare occasions, specimens over 100 cm long and 10 kg in weight are found. Ommanney (1953) reported that the largest *E. affinis* caught during a survey in the Mauritius-Seychelles area was a specimen 87 cm long, which weighed 8.6 kg (19 lb). Around the Marquesas Islands, *E. affinis* as large as 79 cm have been taken on surveys conducted by the NMFS Honolulu Laboratory. Landau (1965) estimated the age of the oldest fish from a sample collected in the Red Sea as 6 yr old. The fish was 62 cm SL and weighed a little over 5 kg (11 lb).

Fowler (1936) indicated that *E. alletteratus* from the West Indies grow to 122 cm. The largest specimen measured by Postel (1956) in the Mediterranean Sea off Tunisia was 101.5 cm, but he noted seeing many exceeding a meter in length. In the tropical eastern Atlantic, the largest specimen measured by Postel (1955a) in Senegal was 94.6 cm. Landau (1965) noted that the oldest *E. alletteratus* in her Mediterranean samples belonged to age group X and was estimated to be about 86 cm SL (defined as the distance from snout to insertion of caudal fin). The world record sport catch for *E. alletteratus* is a specimen 92.07 cm long and weighing 12.24 kg (20 lb) (International Game Fish Association undated).

There is no information on the longevity of *E. lineatus*.

3.32 Hardiness

Not much is known on the hardiness of the three species of *Euthynnus*. In establishing tunas in tanks and ponds for experimental purposes, Tester (1952a) noted that small *E. affinis* 0.4 to 1.4 kg (1-3 lb) became established in these enclosures more readily than yellowfin tuna, *T. albacares*. Once a school of *E. affinis* became established, newly introduced fish started to feed during the second day of confinement. In the experimental tanks maintained by NMFS in Honolulu, *E. affinis* have survived for more than 14 mo (Magnuson 1965). Stevens and Fry (1971) took body temperatures of *E. affinis* that had been in captivity for 2 yr. Calkins and Klawe (1963) stated that the hardiness of *E. lineatus* is similar to that of other tunalike fishes and that "They are hardy enough to be successful in their natural environment, but they can only stand a minimum of handling."

3.33 Competitors

The competitors of *E. affinis* in east African waters include skipjack tuna, small yellowfin tuna, *Auxis thazard*, and a carangid, *Megalaspis cordyla* (Williams 1963). These fishes school together with *E. affinis* off east Africa in the Indian Ocean. In waters around Sri Lanka, *E. affinis* are found in schools together with *A. thazard*, and presumably these two species are direct competitors for food (Williams 1963).

Marchal (1963) stated the *E. alletteratus* competes with species with which it is found such as *A. thazard* and *S. sarda*. He also suggests the dolphins (*Delphinus*) and other cetaceans, *Grampus* and *Globicephala*, as probable competitors.

In the eastern tropical Pacific, *E. lineatus* is found in close association with yellowfin tuna, skipjack tuna, and dolphin fish (*Coryphaena*) that undoubtedly compete with it for food (Calkins and Klawe 1963).

3.34 Predators

In east Africa, *E. affinis* have been found in the stomachs of longline-caught striped marlin, *Tetrapturus audax*, and sharks, *Carcharhinus* spp. (Williams 1963).

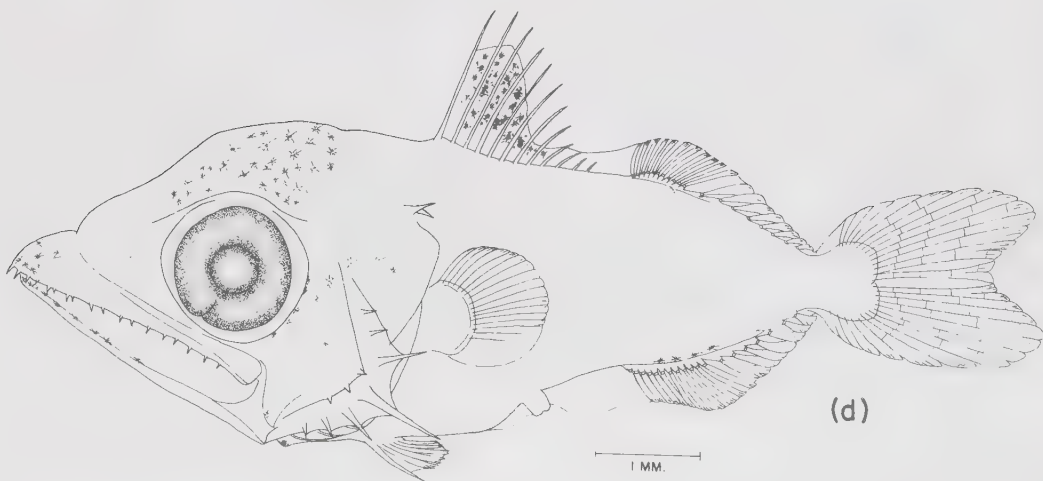
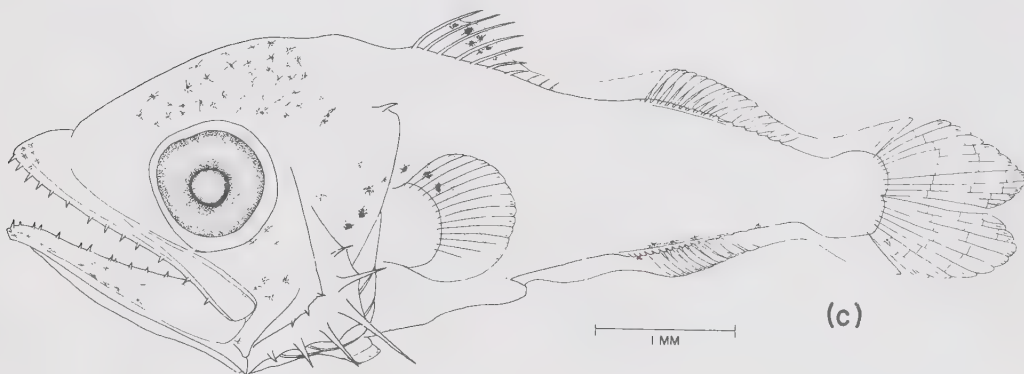
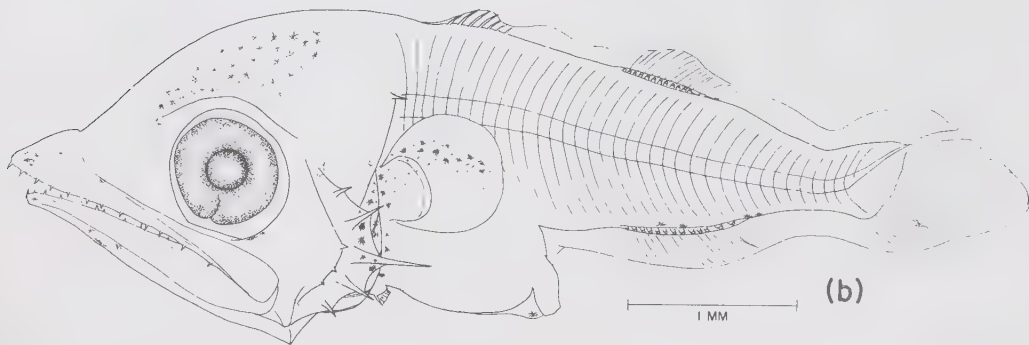
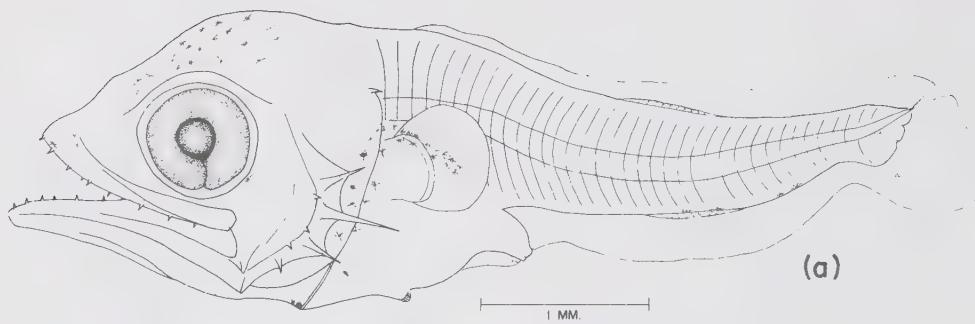
Predators of *E. alletteratus* include various species of sharks, *Carcharhinus* spp. and *Galeocerdo* spp., large yellowfin tuna, and *Istiophorus* spp. (Marchal 1963).

Euthynnus lineatus have been found in the stomachs of yellowfin tuna (Alverson 1963). Calkins and Klawe (1963) stated that the large billfishes undoubtedly prey on *E. lineatus*.

3.35 Parasites, diseases, injuries, and abnormalities

Silas (1967a) and Silas and Ummerkutty (1967) made detailed surveys on parasitism in *Euthynnus* and other

Figure 15.—Postlarvae and juvenile *Euthynnus alletteratus*: (a) 12.0 mm (b) 18.5 mm; (c) 26.0 mm; (d) 58.0 mm. (From Matsumoto 1959, figs. 11-14.) (See Fig. 12 for definition of body length.)



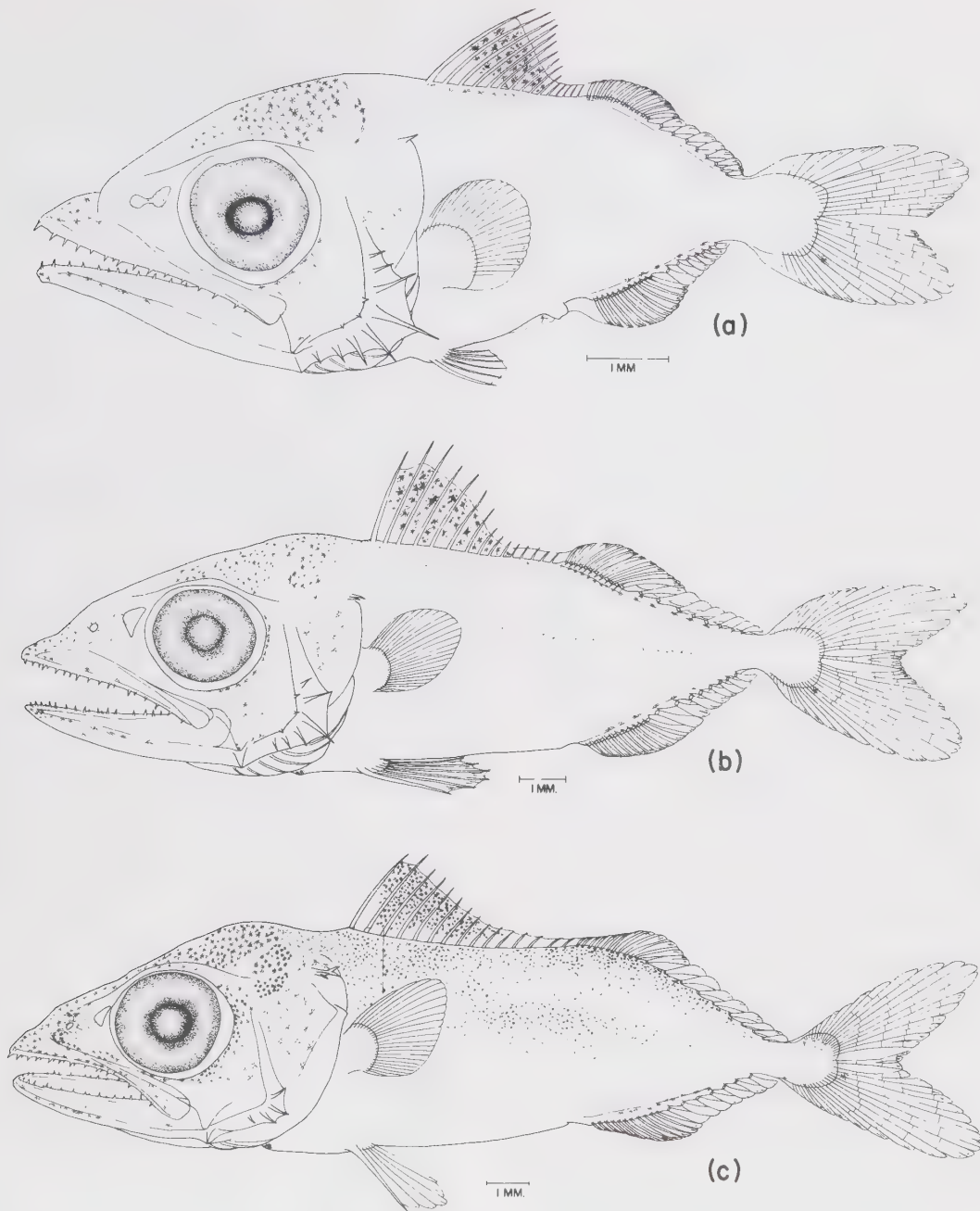


Figure 17.—Postlarval and juvenile *Euthynnus lineatus*: (a) 10.6 mm; (b) 18.6 mm; (c) 21.0 mm. (From Matsumoto 1959, figs. 5-7.) (See Fig. 12 for definition of body length.)

scombrids. They found that the three species of *Euthynnus* were parasitized by various copepods, digenetic trematodes, and monogenetic trematodes (Table 15).

Figure 16.—*Euthynnus lineatus* larvae: (a) 5.0 mm; (b) 6.0 mm; (c) 7.1 mm; (d) 9.3 mm. (From Matsumoto 1959, figs. 1-4.) (See Fig. 12 for definition of body length.)

Calkins and Klawe (1963) also found that *E. lineatus* was parasitized by a trematode *Hirudinella marina*, which was found in the stomach. Postel (1954) also listed the parasites of *E. alletteratus* (Table 16). Thomas (1967) described a new parasitic copepod, *Caligus krishnai*, from the gills of *E. affinis*.

Table 15.—Parasites of *Euthynnus*. (Modified from Silas 1967a; Silas and Ummerkuty 1967.)

Host	Parasites		
	Copepods	Monogenetic trematodes	Digenetic trematodes
<i>Euthynnus alletteratus</i>	<i>Caligus bonito</i> <i>Caligus coryphaenae</i> <i>Pseudocycnus appendiculatus</i> <i>Ceratocolax euthynni</i> <i>Bomolochus anonymous</i>	<i>Capsala maccallumi</i> <i>Capsala manteri</i> <i>Hexostoma macracanthum</i>	<i>Dinurus scomбри</i> <i>Lecithochirum texanum</i> <i>Rhipidocotyle capitatum</i> <i>Rhipidocotyle nagaty</i> <i>Sterrhurus monticelli</i> <i>Tergestia laticollis</i>
<i>Euthynnus affinis</i>	<i>Caligus coryphaenae</i> <i>Caligus regalis</i> <i>Pseudocycnus appendiculatus</i> <i>Caligus bonito</i> <i>Caligus amblygenitalis</i> <i>Caligus euthynnus</i> <i>Caligus asymmetricus</i> <i>Caligus savala</i> <i>Caligus productus</i> <i>Caligulus longispinosus</i>	<i>Capsala gouri</i> ¹ <i>Pricea minimae</i> ¹ <i>Hexostoma euthynni</i> <i>Allopseudaxine katsuwonis</i> <i>Allopseudaxine macrova</i>	<i>Rhipidocotyle septapapillata</i> ¹ <i>Lecithochirum magnaporum</i> ¹ <i>Lecithochirum microstomum</i> <i>Hirudinella marina</i>
<i>Euthynnus lineatus</i>	<i>Caligus coryphaenae</i> <i>Caligus macarovi</i>	<i>Hexostoma euthynni</i>	¹ <i>Lecithochirum magnaporum</i> ¹ <i>Lecithochirum microstomum</i>

¹ Doubtful record.Table 16.—Parasites of *Euthynnus alletteratus*. (From Postel 1954, table 2.)

Parasite	Life stage	Location of infestation
<i>Callitetrarhynchus gracilis</i>	Plerocercoid larvae	Body cavity
Otobothriidae	Plerocercoid larvae	Pyloric caeca
<i>Radiorhynchus pristis</i>	Adult	Stomach
<i>Sterrhurus</i> sp.	Adult	Stomach
<i>Hirudinella clavata</i>	Adult	Stomach
<i>Hexostoma thunninae</i>	Adult	Gills
<i>Hexostoma macrocanthum</i>	Adult	Gills
<i>Nerocila orbignyi</i> form <i>maculata</i>	Adult	Ventral finlets

3.36 Physiology, biochemistry, etc.

Carey et al. (1971) stated that the tunas, including *E. alletteratus*, have evolved a countercurrent heat-exchange mechanism for conserving metabolic heat and raising body temperature. They determined that the temperature of one specimen of *E. alletteratus* was 31.2°C. The surface water temperature was 19.9°C; thus, the body temperature of the fish was 11.3°C higher than the surrounding water temperature.

Stevens and Fry (1971) determined the body temperatures of two *E. affinis* held in captivity for 2 yr. They found that captivity reduced the excess temperature (defined as the body temperature minus ambient water temperature) of *E. affinis*. Graham (1973) determined the thermal profile of *E. lineatus*, which uses a centrally located vascular heat-exchange mechanism similar to that of *E. alletteratus* to maintain core body temperatures warmer than ambient temperature of seawater. He also described the structure of the central heat-exchange mechanism and the effect of temperature changes in blood-gas relationships in *E. lineatus*. Graham found that a warm central core in *E. lineatus* was related to the distribution of red muscle. The warmest body temperatures occurred along the vertebral column between the

first and second dorsal fins. The heat-exchange mechanism in *E. lineatus* was composed of the dorsal aorta, the posterior cardinal vein, and a large vertical rete. The dorsal aorta was embedded in the posterior cardinal vein and was thus completely bathed in venous blood. Graham found that similar to the situation in bluefin tuna, *T. thynnus*, the oxygen-carrying capacity of hemoglobin was unaffected by changing blood temperature. Graham (1975) discussed the adaptive significance of elevated body temperatures in scombrid fishes. He reiterated the observation made by Carey et al. (1971) that the principal advantage of a high and fairly constant body temperature is facilitation of continuous swimming by increasing the frequency of muscular contractions, thus increasing available swimming power. Graham (1975) also observed that warm-bodied fishes probably achieve a marked independence from environmental temperature that permits them to make rapid horizontal and vertical migrations without the necessity of thermal acclimation.

Aspects of gas exchange in *E. affinis* have also been determined (Stevens 1972). The perfusion rate of the gills was determined to be 1.77 liter/min per kg (mean) and ranged from 1.55 to 1.88 liter/min per kg in three trials on a 2.26 kg specimen. The head loss in centimeters of water averaged 1.8. The calculated resistance to water flow offered by the gills averaged 1.03 cm of water/min per kg per liter and ranged from 0.90 to 1.20. Oxygen uptake was determined to be 503 mg/h per kg (mean) and ranged from 400 to 643. The calculated utilization (fraction of oxygen removed from the water) averaged 0.79 and ranged from 0.69 to 0.95.

Rivas (1953) determined that scombrid fishes, including *Euthynnus*, possessed a pineal apparatus. He gave a description of the pineal apparatus and hypothesized that it might function as a light receptor to control phototactic movements of the fish. Support for Rivas' hypothesis was provided by Murphy (1971) who investi-

gated the pineal organ in bluefin tuna and found that the bluefin tuna's pineal organ had sensory cells possessing the structural characteristics of vertebrate retinal photoreceptor cells. He concluded that the pineal organ in bluefin tuna serves as a photoreceptor which receives external light stimuli and that such stimuli may travel from the pineal organ to a site of action via an apocrine secretion moving through capillaries or more likely by impulses transmitted by the pineal nerve.

Magnuson (1970) made a detailed study of the hydrostatic equilibrium of *E. affinis*. This study was based on morphometric and body density measurements of fish 31.6 to 67.8 cm long and from observations on the swimming behavior of fish about 42 cm long held in tanks. Variations in required lift under various conditions of seawater density, density of fish, and amount of food in the gut were evaluated. Magnuson (1970) also estimated the effectiveness of each lifting hydrofoil on *E. affinis* in terms of the percentage of the total lift it produced, its surface loading, and its coefficient of lift. He used all these parameters to develop a model which predicted the minimum speed required for hydrostatic equilibrium. In a later paper Magnuson (1973) tested this model to see if it predicted the swimming speeds of a large number of scombroid fishes, including *E. affinis*; considered the "adaptive radiation in the morphology especially of the gas bladder and pectoral fins which together with swimming speed contribute to the mechanism by which scombroids maintain hydrostatic equilibrium"; and considered problems associated with maintaining hydrostatic equilibrium by large body size.

3.4 Nutrition and growth

3.4.1 Feeding

Observations on various aspects of feeding and related observations have been made on *Euthynnus*. Bullis and Juhl (1967) observed what they called "phalanx orientation" in the feeding behavior of *E. alletteratus* near the Grenadine Islands in the Lesser Antilles. This pattern of orientation was observed as the *E. alletteratus* were apparently feeding on a large group of dwarf herring, *Jenkinsia lamprotaenia*, which had collected directly under a floating night light. The phalanx developed by a single fish being joined by another and then by a third fish. This phalanx took the form of a tightly packed three-fish aggregation evenly aligned side by side. The phalanx attacked the ball of dwarf herring without altering formation. The observers noted that the attack on the dwarf herring did not start until the phalanx had been formed. During the course of feeding, additional *E. alletteratus* were seen to join the phalanx until it was estimated that the phalanx contained 14 or 15 fish of about the same size.

Wicklund (1968) reported on daylight feeding patterns of *E. alletteratus* in Florida waters. He observed a school of 20 and a group of 4 fish feeding on bigeye scad, *Selar crumenophthalmus*, and herring, *Clupea* sp. Wicklund

observed *E. alletteratus* moving toward the herring at which time the herring moved to the bottom and mixed with the scad. The *E. alletteratus* attacked when all the herring and scad were tightly packed against the bottom. In their attacking maneuver, the fish swam downward toward their prey with a great burst of speed and in the instant before reaching bottom they turned sharply parallel to the bottom, stirring up clouds of sediment. Wicklund noted that the *E. alletteratus* took their prey at this point or a fraction of a second later, and noted that the fish's jaws could be heard snapping audibly. The feeding continued all day, presumably in the same manner. The *E. alletteratus* left the area in the evening at 1800 and returned at 1030 the next day.

Wicklund's (1968) observations have similarities and differences from observations made by Hiatt and Brock (1948). The latter observed a group of three *E. affinis* herding a closely packed school of several hundred scads, *Decapterus sanctaehelenae*, over a large coral head in Rongerik lagoon in the northern Marshall Islands. They noted that the three *E. affinis* "... usually followed the school of scads rather closely, with one tuna at each rear flank of the school and the third lagging behind them. Now and then the scads would turn off to one side, at which time the tuna on that side could move forward swiftly and herd them back into line." On one occasion, Hiatt and Brock (1948) saw a stray scad eaten by the rearmost *E. affinis*. Except for this incident, the *E. affinis* did not make any attempt to prey on the scads during the 3-h observational period. Wicklund's observations were similar to Hiatt and Brock's in that in both instances the *Euthynnus* forced the prey into tightly packed schools. However, the *E. alletteratus* observed by Wicklund (1968) aggressively attacked their prey whereas the *E. affinis* observed by Hiatt and Brock (1948) merely picked off the stragglers. In this regard, Wicklund's observations are more similar to those made by Kishinouye (1923). Kishinouye (1923) noted that *E. affinis* were voracious feeders, and described their feeding method as darting swiftly into a school of small fish and scattering them. As Kishinouye (1923) stated, however, the feeding habits of *E. affinis* may vary throughout the year. Presumably, this could also be true for the other species of *Euthynnus*.

Walters (1966) studied the filter feeding of *E. affinis* by means of high-speed motion pictures. He showed that *E. affinis* traveled an average of 5.9 body lengths/s while feeding and observed a maximum speed of 10.0 body lengths/s. He found no change in speed and no increase in swimming effort as the fish opened its mouth and distended the orobranchial chamber to engulf its prey. Walters (1966) observed that the feeding mechanism is drag free and that *E. affinis* feeds by swimming over its prey rather than by sucking it into its mouth. He also pointed out that *E. affinis*, and scombrid fishes in general, are facultative filter-feeders in that they are able to feed in open water upon swimming organisms that are minute in comparison to the size of the predator, and noted the high gill-raker counts in these species to support his statement.

Magnuson and Heitz (1971) determined that the mean gill-raker gap for *E. affinis* was 1.4 mm and the filtering area of the first gill arch was 650 mm². They noted that in terms of gill-raker gap, *E. affinis* was intermediate (ranked fifth, going from small to large) compared with *Katsuwonus pelamis*, *Auxis rochei*, *A. thazard*, *Scomber japonicus*, *Thunnus albacares*, *T. alalunga*, *T. obesus*, *Sarda chiliensis*, *S. orientalis*, *Coryphaena equiselis*, and *C. hippurus*, ranked from small to large, respectively. Magnuson and Heitz (1971) related the gill-raker apparatus to food selectivity among these fishes and noted that despite the varied diet of scombrid fishes, selectivity in terms of size does exist in the scombrids. They observed that within a species, larger fish fed on relatively fewer crustaceans and more fishes.

3.42 Food

Observations on the diet of *Euthynnus* from various localities suggest that these fishes feed primarily on whatever is available at any particular place and time. As an example Ronquillo (1953) found that *E. affinis* fed about equally on crustaceans (56.2% by number) and fishes (43.8% by number) in Philippine waters. Ronquillo (1953) found no squids in the stomachs. Around Hawaii Tester and Nakamura (1957) also found that squids were negligible in the diet of *E. affinis*, but unlike the Philippine area, fishes were much more important (91.8% by volume) than crustaceans (8.2% by volume). In the Indian Ocean, Kumaran (1964) found that squids (56.5% by volume) were most important, followed by fishes (38.3% by volume), and crustaceans (5.2% by volume) were the least important.

For *E. alletteratus* in the Mediterranean Sea, Oren et al. (1959) found that crustaceans (63% by number) were most important followed by fishes (22% by number) and squids (11% by number). Heteropods and tunicates made up 4% by number of the diet.

Small fish; squid; *Auxis thazard*; a pelagic crab, *Pleuroncodes planipes*; and sierra mackerel, *Scomberomorus sierra*, have been found in the stomachs of *E. lin-eatus* (Calkins and Klawe 1963).

Table 17 presents examples of food items found in stomachs of *Euthynnus* from various areas. It can be seen in Table 17 that Postel (1954) listed *E. alletteratus*, presumably a juvenile, from the stomach of an adult *E. alletteratus*.

3.43 Growth rate

Euthynnus affinis

The available information on the age and growth of *E. affinis* is sketchy and fragmentary. No data are available on the growth of the larvae. On the juveniles, Kishinouye (1923) suggested that a 115 mm specimen caught off Port Keelung in August may have been about 3 mo old. Wade (1950a) speculated that a 115 mm long specimen from the Celebes Sea was 3 or 4 mo old, and that a 175 mm specimen may have been spawned as long as 6

Table 17.—Food of *Euthynnus* spp.

Food items	Number of food organisms	Percentage prevalence	Percentage by volume
Food of <i>Euthynnus affinis</i> . (From Kumaran 1964, table 1.)			
Crustacea:		(20.4)	(5.2)
Isopods	7	2.8	—
Amphipods	9	2.8	—
Copepods	9	3.4	0.1
<i>Penaeus</i> sp.	3	1.4	0.1
Phyllosoma larvae	6	2.7	0.1
Megalopa larvae	8	2.0	0.1
<i>Squilla</i> sp.	2	0.7	—
<i>Alima</i> larvae	82	5.5	3.4
Unidentified crustaceans	17	5.5	1.1
Gastropoda:			
Pteropods	5	1.4	—
Cephalopoda:		(12.3)	(56.5)
<i>Sepioteuthis</i> sp.	25	10.9	55.7
<i>Loligo</i> sp.	2	1.4	0.8
Vertebrata (Pisces):		(87.1)	(38.3)
<i>Sardinella</i> spp.	10	5.5	0.7
<i>Stolephorus commersonii</i>	15	6.8	1.0
<i>Anchoviella tri</i>	56	23.7	3.4
Other clupeids	6	3.4	0.5
<i>Saurida</i> sp.	4	2.0	0.4
<i>Leptocephalus</i>	3	1.4	0.1
<i>Hemiramphus</i> sp.	1	0.7	—
<i>Holocentrus</i> sp.	3	1.4	0.6
<i>Sphyræna</i> sp.	5	2.7	—
<i>Sillago sihama</i>	7	4.1	0.4
<i>Lactarius lactarius</i>	1	0.7	0.1
Carangids	18	5.5	13.8
<i>Leiognathus</i> spp.	141	32.5	6.8
<i>Sciaena</i> sp.	1	0.7	—
<i>Euthynnus affinis</i>	1	0.7	—
<i>Triacanthus</i> sp.	1	0.7	0.2
Unidentified fish including larvae	36	14.9	9.5
Food of <i>Euthynnus alletteratus</i> . (From Postel 1954, table 1.)			
Fish:			
<i>Sardinella aurita</i>	<i>Smaris</i> sp.		
<i>Sardinella</i> sp.	<i>Ammodytes</i> sp.		
<i>Engraulis</i> sp.	<i>Galeiodes polydactylus</i>		
<i>Aulopus</i> sp.	<i>Scomber japonicus</i>		
<i>Saurida parri</i>	<i>Auxis</i> sp.		
<i>Myctophum</i> sp.	<i>Euthynnus alletteratus</i>		
<i>Fodiator acutus</i>	<i>Caranx Rhoncus</i>		
<i>Cypselurus</i> sp.	<i>Decapterus pundtatus</i>		
Hemiramphidae	<i>Vomer Setipinnis</i>		
<i>Sphyræna</i> sp.	<i>Pagellus</i> sp.		
<i>Box boops</i>	<i>Sargus</i> sp.		
Molluscs:			
Shelled (?) molluscs			
<i>Sepia</i> sp.			
<i>Loligo</i> sp.			
<i>Allotenthis africana</i>			
Crustacea:			
Planktonic crustacea			
Euphausiacea			
Sergestidae			
<i>Parapeneus longirostris</i>			
Bryozoans			
Madreporaires			
Green algae			

mo before its capture. These observations suggest a growth rate of 1.0 to 1.3 mm/day.

Yabe et al. (1953) presented length data of preadult *E. affinis* landed at the port of Aburatsu, Japan, during

August-October 1950 (Table 18; Fig. 18). Yabe et al. indicated that *E. affinis* between 150 and 250 mm were in their first year of life. Figure 18 suggests an average growth rate of 1.5 mm/day. This growth rate is not very different from that suggested for *E. affinis* juveniles in the Philippines.

Ommanney (1953) observed the age-size relationship of *E. affinis* caught near the Seychelles. Although the basis for determining the age-size relationship is not made clear, he suggested that postlarval to 25 cm fish

Table 18.—Average size of *Euthynnus affinis* landed at Aburatsu, Japan. (From Yabe et al. 1953, table 5.)

Month	No. of fish measured	Fork length (mm)	
		Range	Mean
Aug.	26	107	183-240
	30	51	201-225
	31	98	203-239
Sept.	1	53	194-240
	2	19	199-268
	4	92	209-245
	5	78	204-290
	6	91	200-309
	7	79	203-307
	8	132	196-325
	9	149	200-271
	20	115	213-274
	25	13	223-255
Oct.	6	5	230-295
	11	9	252-278
	13	24	254-286
	16	138	244-313
	17	111	220-332

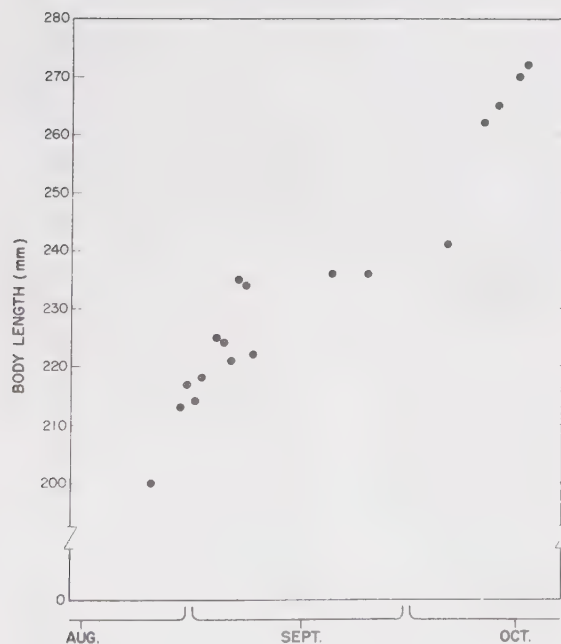


Figure 18.—Growth of preadult *Euthynnus affinis* off the southern coast of Japan. (Data from Yabe et al. 1953.)

were in their first year of life, 25 to 45 cm fish in their second year, 45 to 65 cm fish in their third year, and 65 cm and larger fish in their fourth year and over.

Landau (1965) determined the ages of *E. affinis* from the southern Red Sea based on the annular marks on the vertebral centra. The age-size relationships are given in Table 19. Landau, using the graphical method, estimated that the L_{∞} for *E. affinis* in the Red Sea was 580 mm SL.

Table 19.—Age-size relationships of *Euthynnus affinis* from the Red Sea. (From Landau 1965, tables 2, 3.)

Age	No. of fish	Length (SL) ¹ in mm		Approximate mean weight (kg)
		Range	Mean	
Southern Red Sea (April-June 1964)				
I	28	310-430	345	0.9
II	11	370-520	456	2.1
III	18	470-560	511	2.8
IV	25	520-590	544	3.3
V	10	520-600	554	3.5
Bay of Eilat, Red Sea (May 1964)				
I	78	320-340	370	1.0
II	2	505 and 525	—	3.0

¹SL is standard length defined by the author as the distance from the snout to the insertion of the caudal fin.

On the basis of annular marks on the first dorsal spine of *E. affinis*, Shabotinets (1968) determined the age-size relationship of fish taken in the Gulf of Aden as shown below.

Age	Size (cm)
3	50-65
4	55-75
5	65-80
6	86

Euthynnus alletteratus

Houde and Richards (1969) observed the growth of larval *E. alletteratus* under laboratory conditions. They collected fertilized eggs in the western edge of the Gulf Stream near Miami, Fla., and incubated and hatched the eggs in 20- and 140-gal (75.5- and 530-liter) aquaria. The growth in length of the larvae in one of their rearing experiments is shown in Figure 19. As can be seen the larval fish grew from approximately 2.5 mm to a little less than 8.5 mm in 18 days. Houde and Richards noted that the growth of the larvae was probably not as fast as in the natural environment.

Based on modal groups in length-frequency distributions Postel (1955b) presented the following age-length relationships for *E. alletteratus* off Dakar in the eastern Atlantic:

Less than 1 yr (Group 0)	<30 cm
1 to 2 yr (Group 1)	30-45 cm
2 to 3 yr (Group 2)	45-60 cm
3 to 4 yr (Group 3)	60-75 cm
Over 4 yr	>75 cm

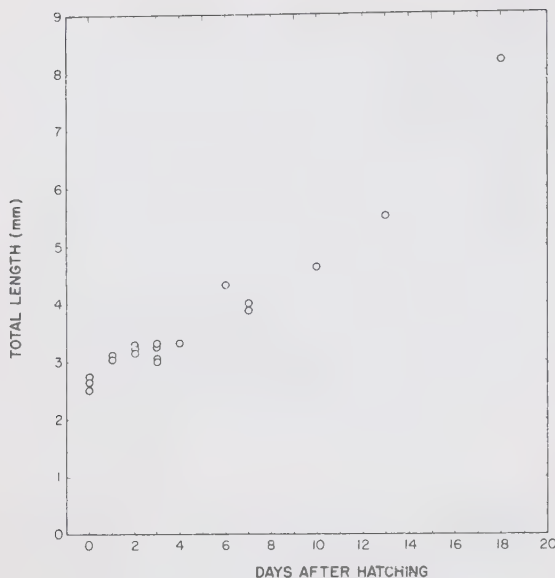


Figure 19.—Growth in length of *Euthynnus alletteratus* larvae reared in the laboratory. (From Houde and Richards 1969, fig. 3.)

Landau (1965) determined the ages of *E. alletteratus* in the Mediterranean Sea by reading marks on the vertebral centra. Lengths of fish at various ages were back-calculated by relating the radius of annular marks on the vertebrae to the length by the regression:

$$LS = 45.85V + 72.62$$

where *LS* is standard length defined as distance from snout to insertion of caudal fin, and *V* is vertebral radius. The age-size relations determined by Landau are given in Table 20. Landau also estimated L_{∞} for *E. alletteratus* as 840 mm, using the graphical method on size obtained by back-calculations.

Euthynnus lineatus

Except for some observations on the growth of juvenile *E. lineatus* there is nothing in the literature on the growth of this species. Clemens (1956) was able to rear juvenile *E. lineatus* for up to 10 days in shipboard aquaria. From the beginning of the holding experiment to the end 10 days later, the average weight of the juveniles increased 11 times and the average length increased approximately 1.4 times (Table 21).

Table 20.—Age-length and age-weight relationships for *Euthynnus alletteratus* in the Mediterranean Sea. (From Landau 1965, table 1.)

Age	Length (SL) ¹ in mm		Approximate mean weight (kg)
	Range	Mean	
I	28-49	358.4	0.8
II	46-68	539.1	2.8
III	54-75	637.2	4.5
IV	61-79	701.9	6.0
V	65-84	755.0	7.5
VI	74-86	801.5	8.5
VII	75-84	810	9.0

¹SL is standard length defined by the author as the distance from the snout to the insertion of the caudal fin.

3.44 Metabolism

Malvin and Vander (1967) determined the plasma renin activity in *E. affinis*. They pointed out that there is general agreement that freshwater fishes contain renin in their kidneys but that this problem had not been resolved in marine fishes; furthermore, plasma renin had not been measured for marine species. Their results showed that certain characteristics in the plasma renin activity of *E. affinis* and *K. pelamis* were identical to that of the mammalian renin-angiotensin system which strongly indicated to them that the material being evaluated was angiotensin generated by the enzymatic action of renin. It was determined that the renin activity, expressed as angiotensin-equivalents, was 23.3 and 15.8 ng/ml of plasma for two specimens of *E. affinis*.

Klawe et al. (1963) determined the hemoglobin content of the blood of *E. lineatus*. They noted that the hemoglobin content of the blood of fishes is generally related to the level of activity of the species. The hemoglobin concentration of *E. lineatus* blood ranged from 16.9 to 19.9 g/100 ml for five fish measuring 427 to 657 mm. This level of hemoglobin concentration was higher than for *Scomber japonicus* and *Sarda chiliensis*. They speculated that the higher hemoglobin content of the blood of *E. lineatus* was somehow related to its complex cutaneous vascular system which *S. japonicus* and *S. chiliensis* lack.

3.5 Behavior

For feeding behavior, see section 3.4; for reproductive behavior, see section 3.13.

Table 21.—Growth of postlarval *Euthynnus lineatus*. (From Clemens 1956, table 1.)

Number of fish	Hours ¹		Standard length (mm)		Fork length (mm)		Weight (g)	
	Range	Average	Range	Average	Range	Average	Range	Average
23	0	0	17.0-37.5	26.8	18.5-40.0	28.3	0.10-0.57	0.29
3	171-175	173	48.0-52.0	49.3	51.0-55.0	52.0	1.51-1.91	1.70
3	194-200	197	54.0-55.0	54.3	58.0	58.0	1.94-2.37	2.14
4	244-248	246	59.0-71.5	63.6	63.0-75.0	67.5	2.61-4.72	3.46

¹Hours of growth computed from time fish started feeding, 42 h after capture.

3.51 Migrations and local movements

See section 5.3.

3.52 Schooling

Aspects of the schooling behavior of *Euthynnus* relative to feeding have been discussed in section 3.41. Other observations on the schooling behavior of *Euthynnus* indicate that these species tend to school with other species. In the Indian Ocean off the east African coast, *E. affinis* were found in schools with small *T. albacares*, *K. pelamis*, *Auxis* sp., and a carangid, *Megalaspis cordyla* (Williams 1963). Williams noted, however, that all individuals in the schools were of much the same size. He also found that with small *E. affinis* "the schooling is strong and disciplined."

Elsewhere in the Indian Ocean, Williams (1963) noted that in waters around Sri Lanka, mixed schools of *Auxis* spp. and *E. affinis* are common. Sivasubramaniam (1970) stated that *K. pelamis*, *Auxis* spp., and young *T. albacares* occur together with *E. affinis* and that the catches are almost always mixed. Fourmanoir (1957) observed that around Madagascar, schools of *E. affinis* were almost always distinct from that of other species of tuna, except in June to the east of Nosy-Bé, where *T. albacares* were taken at the same time as *E. affinis*.

Williams (1963) noted that in east Africa, schools of *E. affinis* were composed of 100 to 1,000 or more individuals, and in Sri Lanka as many as 5,000 individuals (mixed *E. affinis* and *Auxis* spp.) may be taken in one haul of a beach seine.

Cahn (1972) investigated side-to-side spacing and positional orientation of *E. affinis* during schooling in experimental tanks. The study was designed to demonstrate the role of the lateral line sensory system in the schooling of *E. affinis*. *Euthynnus affinis*, in the experimental tanks, significantly increased their side-to-side spacing and altered their diagonal to abeam position ratios so that the abeam orientation assumed increased importance when the hydrodynamic field between orienting fish was blocked by a transparent partition. She concluded that hydrodynamic contact is essential for the typical spacing and positional orientation in schooling, and that the lateral line plays a prime regulatory role as the water turbulence detector.

Although *E. alletteratus* are found in schools most of the time, they have a tendency to scatter during certain periods of the year (Marchal 1963). Marchal further noted that *E. alletteratus* schools have an elliptical shape of variable size and may be as long as 30 m along the long axis. Like *E. affinis*, *E. alletteratus* often school with other species, including *Auxis* sp., *Sarda sarda*, and *Selar crumenophthalmus*. All the individuals in these mixed schools tend to be of the same size (Marchal 1963).

Euthynnus lineatus in Peruvian waters are frequently found in schools with *T. albacares* and *K. pelamis* of the same size (Bini 1952). The number of individuals in the school, however, was not as great as the commercially important species. Calkins and Klawe (1963) reported that commercial tuna fishermen have observed that *E.*

lineatus will frequently collect around drifting or anchored tuna boats. They noted that *T. albacares* and *K. pelamis* also exhibit this type of behavior but believed this behavior pattern was more pronounced with *E. lineatus*. Hunter and Mitchell (1967) observed schools of *E. lineatus* beneath flotsam or drifting objects. However, these schools remained near the floating objects only for short periods and they did not swim as close to the objects as did other small fishes. They could not ascertain whether the schools of *E. lineatus* were truly associated with a particular object.

3.53 Responses to stimuli

Tester (1959) summarized the various experiments on the response of *E. affinis* and other tunas to stimuli (Hsiao 1952; Miyake 1952; Tester 1952a, 1952b; Van Weel 1952; Tester et al. 1954; Hsiao and Tester 1955; Tester et al. 1955; Miyake and Steiger 1957). It was found that *E. affinis* were attracted to continuous white light over a range of moderate intensity (about 70 to 450 fc). *Euthynnus affinis* were not attracted to a light of weaker intensity, and were repelled by a light of stronger intensity (Hsiao 1952). In experiments testing the reaction of *E. affinis* to moving objects of various colors, it was found that white lures were slightly more attractive than red, black, or silver (Hsiao and Tester 1955). Hsiao and Tester (1955) noted, however, that this may have been associated with greater visibility than color preference. Experiments on the chemoreception of *E. affinis* indicated that this species had a well-developed sense of smell or taste in that they were strongly attracted to clear colorless extracts of tuna flesh. It was further found that the attractant was contained in the protein rather than the fat fraction of the clear extract (Van Weel 1952; Tester et al. 1955). It was also determined that *E. affinis* became conditioned to the smell of juices exuded from the food which presumably contained common or similar substances which stimulated the feeding response (Tester et al. 1954).

Nakamura (1968) determined the visual acuity of *E. affinis*. Visual acuity was defined as the ability to see clearly the fine details of objects, especially as the objects become smaller and closer together. To determine the visual acuity, *E. affinis* were trained to discriminate between vertically and horizontally striped images that were projected on an opal glass plate in an experimental tank. The visual acuity of two *E. affinis*, 36.4 cm (0.9 kg) and 43.4 cm (1.6 kg), were determined at various levels of luminance (Fig. 20). Nakamura (1968) also conducted these experiments on *K. pelamis* and noted that at lower luminances the visual acuity of the two species were similar. At higher luminances, however, *K. pelamis* had a greater visual acuity than *E. affinis*.

Experiments have also been conducted to describe the hearing thresholds and frequencies audible to *E. affinis* (Iversen 1969). Based on experiments with two specimens, Iversen determined a threshold curve for acoustic sound pressure for *E. affinis* which showed that the fish perceived sounds from 100 to 1,100 Hz (Fig. 21). The

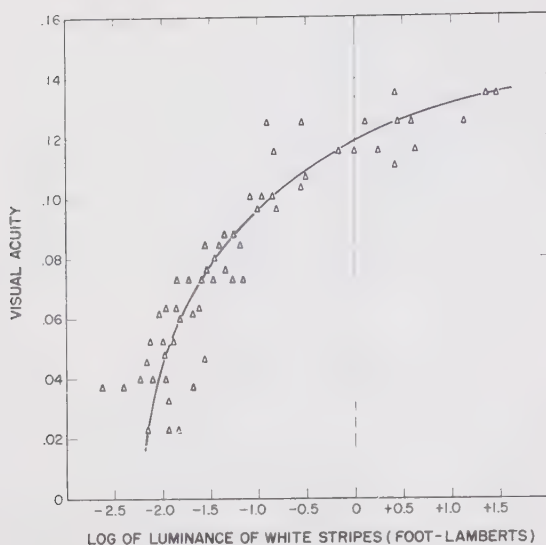


Figure 20.—Visual acuity curve of *Euthynnus affinis* at adaptive illumination of 170 luxes. Curve fitted by eye. (From Nakamura 1968, fig. 3.) (Although not explicitly stated, it is believed that visual acuity is plotted against log_e of luminance.)

lowest mean threshold was 7 dB/mbar at 500 Hz. At 100 Hz the threshold was 30 dB/mbar higher than at 500 Hz, and at 1,100 Hz it was 23 dB/mbar higher. The mean thresholds for *E. affinis* were consistently higher than those for *T. albacares* (Iversen 1967). Iversen (1969) noted that this difference could have resulted in part from the lack of a gas bladder in *E. affinis*.

Steffel et al. (1976) conducted experiments on captive *E. affinis* to determine their ability to discriminate temperature gradients. Tests on two fish yielded a discrimination threshold of 0.10° to 0.15°C. Their experiments indicated that the thermal sensitivity of *E. affinis* is no more acute than that of inshore fishes and appeared inadequate for direct sensing of weak horizontal temperature gradients at sea.

Walters (1966) determined the swimming speed of *E. affinis* by high-speed motion pictures. He observed that *E. affinis* traveled an average of 5.9 body lengths/s while feeding and a maximum of 10.0 body lengths/s. The non-feeding swimming speed, with food present, averaged 4.5 body lengths/s and ranged from 2.9 to 12.5 body lengths/s.

Magnuson (1969) investigated the swimming activity of captive *E. affinis* as related to their search for food in outdoor tanks. He determined that the average swimming speed of *E. affinis*, averaging about 35 cm long, was 80 cm/s during the day and 83 cm/s at night in tanks containing no food. These fish had been in captivity for less than a month. Swimming speed measurements made after the fish had been in captivity for 5 to 6 and 8 mo showed that the speed was lower than that of fish held less than a month, but no marked difference was observed between the mean speed during the day (74 cm/s) and the mean speed during the night (72 cm/s). Magnuson (1969) also measured the swimming speed of

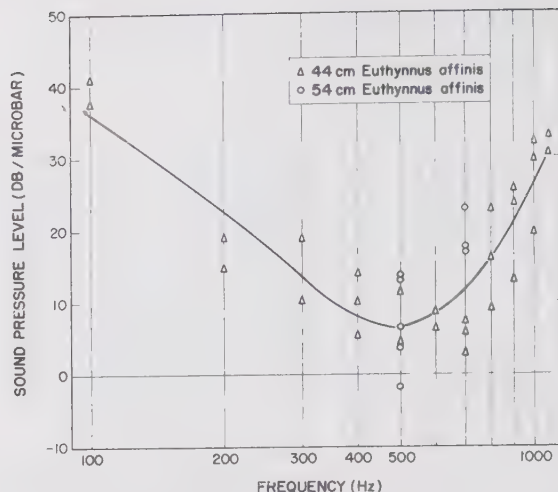


Figure 21.—Acoustic sound pressure thresholds of two *Euthynnus affinis*. (From Iversen 1969, fig. 1.)

E. affinis in tanks containing several thousand live prey fish. They appeared to swim faster than those without food, averaging 108 cm/s during the day and 92 cm/s at night. He noted that the higher day speeds were caused from intermittent high-speed pursuit of the prey. *Euthynnus affinis* did not prey on the baitfish at night.

Magnuson (1969) found that swimming speed was highest after a meal and decreased when the fish were deprived of food. He argued that if the level of swimming activity is regulated by search for food, swimming speed should be higher when motivation to feed is increased by deprivation of food. Because swimming speed decreased during deprivation, he concluded that swimming activity must be regulated in response to some biological need other than food search. He further concluded that swimming activity appeared to be more closely related to the requirements for maintaining hydrostatic equilibrium and gill ventilation, than for food search.

Inoue et al. (1970) also made observations on the swimming speed of *E. affinis*. They found that *E. affinis* swam at a speed of 0.30-1.27 m/s during the day and 0.33-0.75 m/s under artificial lights in their experimental tanks 4 m in diameter and 0.6 m deep.

Nakamura and Magnuson (1965) gave a detailed description of the coloration of living *E. affinis*. In addition to the permanent coloration, *E. affinis* exhibited three transient color patterns or markings that were related to feeding. These patterns or markings were black spots ventral to the pectoral fins, faint vertical bars on the flanks, and a yellowish middorsal stripe. These three color patterns were observed when *E. affinis* were feeding. Nakamura and Magnuson (1965) suggested that these transient color patterns may act as "social releasers" to signal the presence of food to other members of the school.

Wickham et al. (1973) investigated the efficacy of midwater artificial structures for attracting pelagic sport fishes in the Gulf of Mexico near Panama City, Fla. With

equal experimental fishing effort they obtained significantly greater catches of *E. alletteratus* around the artificial structures than in adjacent control areas. However, they noted that *E. alletteratus* were seldom observed or captured at the structures unless baitfish were present. They concluded that *E. alletteratus* apparently were not attracted by the structures per se, but rather by the presence of the baitfishes that were attracted to the structures.

4 POPULATION

4.1 Structure

4.1.1 Sex ratio

The sex ratios of *E. affinis* in various localities are given in Table 22. Williamson (1970) estimated the sex ratio of *E. affinis* by size near Hong Kong. He found that for fish from 38 to 49 cm the sexes appeared to be represented in equal numbers but for fish from 50 to 73 cm, 67% of the fish were males.

The sex ratio of *E. alletteratus* in various localities is given in Table 23.

No information is available on the sex ratio of *E. lineatus*.

Table 22.—Sex ratio of *Euthynnus affinis*.

Locality	Sample size	Number (percent)		Source
		Males	Females	
East Africa (western Indian Ocean)	11	6(54.5)	5(45.4)	Morrow (1954)
East Africa (western Indian Ocean)	37	22(59.4)	15(40.5)	Williams (1964)
Hawaii	93	45(48.4)	48(51.6)	Tester and Nakamura (1957)
Philippines	456	243(53.3)	213(46.7)	Wade (1950b)

Table 23.—Sex ratio of *Euthynnus alletteratus*.

Locality	Sample size	Number (percent)		Source
		Males	Females	
Between North Carolina and northern Florida	227	121(53.3)	106(46.7)	de Sylva and Rathjen (1961)
Miami, Fla.	550	261(47.5)	289(52.5)	de Sylva and Rathjen (1961)
Barbate and Tarifa, Spain	378	198(52.4)	180(47.6)	Rodríguez-Roda (1966)
Senegal	866	432(49.9)	434(50.1)	Postel (1955b)

4.1.2 Age composition

See section 4.13.

4.1.3 Size composition

Euthynnus affinis

The length-frequency distribution of *E. affinis* caught by trolling and drift nets in the southwest region of the Sri Lanka fishery is shown in Figure 22. The *E. affinis*

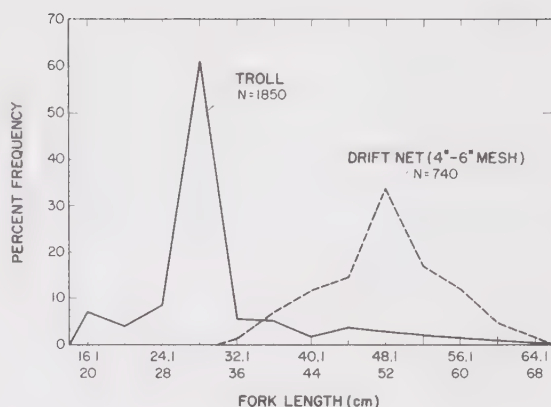


Figure 22.—Length frequencies of *Euthynnus affinis* caught by drift nets and troll lines in the southwest regions of Sri Lanka. (From Sivasubramaniam 1970, fig. 3.)

taken by the commercial fishery ranges from 20 to 65 cm. Occasionally fish in the 15 to 20 cm and 65 to 68 cm groups are also taken (Sivasubramaniam 1970). Sivasubramaniam discussed the size selectivity of the various gear used in the Sri Lanka fishery. He noted that the trolling gear sampled a wide range of sizes of *E. affinis*. However, he also stated that trolling gear selected a larger proportion of smaller sizes of fish in the stock. Although drift nets are highly selective, the use of a wider range of mesh sizes from 10.2 to 15.2 cm (4-6 in) in Sri Lanka made these nets less selective. He indicated that the use of 10.2 to 15.2 cm mesh nets resulted in the capture of a fairly wide size range of *E. affinis*. Since the pole-and-line fishing method is directed primarily at *K. pelamis* which range from 40 to 55 cm, this fishing method tends to select *E. affinis* of the same size range which are found together with *K. pelamis*. Finally, Sivasubramaniam (1970) pointed out that the selectivity of longline gear relative to the size and behavior of *E. affinis* eliminated this species from longline catches. It appears that in general all the various life stages of *E. affinis* occupy the same habitat, and the size of fish taken is primarily dictated by the gear used. This probably holds true for the other two species of *Euthynnus* which are also coastal fishes.

The length-frequency distribution of *E. affinis* caught by trolling along the southeast coast of India is shown in Figure 23. The *E. affinis* caught during July 1960 in this area ranged from about 42 to 68 cm. No modes were discernible in the length distribution. The August 1961 sample showed a mode at around 46 cm and the September 1961 sample at around 52 cm. As noted earlier, other fishing gear in addition to trolling gear are used to catch *E. affinis* along the southeast coast of India. Presumably, the length-frequency distribution of *E. affinis* caught by other gear would differ from that of fish caught by trolling.

The length range of *E. affinis* caught along the southwest coast of India is given by Bennet (1964) (Table 24). The gear used in this fishery includes drift nets and hook and line (presumably trolling gear). Shore seines are oc-

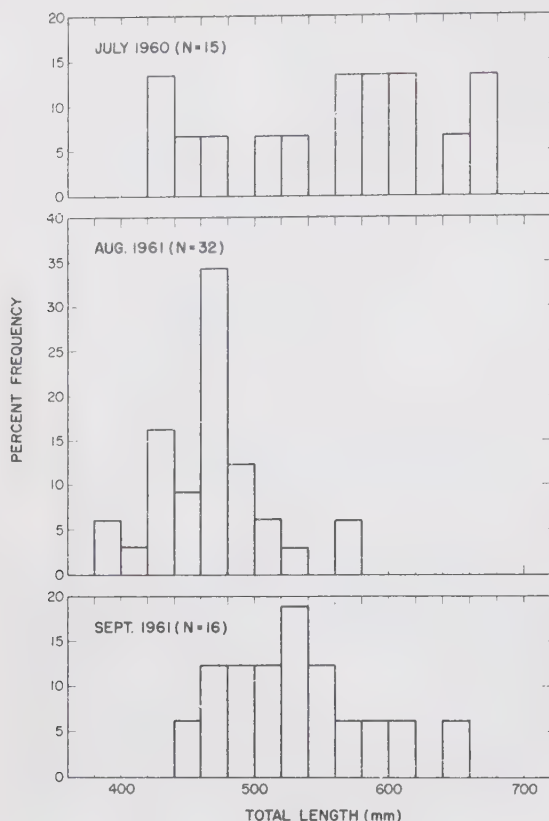


Figure 23.—Length frequencies of *Euthynnus affinis* caught by trolling off the southeast coast of India. (From Silas 1967b, fig. 15.)

Table 24.—Size composition of *Euthynnus affinis* from the southwest coast of India. (From Bennet 1965, table 3.)

Month	Minimum length (cm)	Maximum length (cm)	Month	Minimum length (cm)	Maximum length (cm)
1960			1961		
July	45.0	60.5	January	30.5	62.8
August	43.5	64.0	February	31.7	58.5
September	43.0	60.0	March	24.3	62.3
October	15.0	62.3	April	30.1	70.1
November	24.7	55.0	May	42.5	67.3
December	26.3	62.7	June	42.5	63.7
			July	48.2	66.1
			August	41.6	67.3
			September	42.2	61.0
			October	20.3	59.0

casionally used. The fish caught during the sampling period measured from 15 to 70 cm. Bennet (1964) noted that the smallest fish were taken in October 1960 by shore seine. He further stated that the smaller sizes are not represented in the commercial catches. The size range and the modal groups of *E. affinis* caught in various other localities in the Indian Ocean as summarized by Williams (1963) are shown in Table 25.

Length-frequency data on *E. affinis* caught in Japanese waters are scanty. Yabe et al. (1953) presented size data on young *E. affinis* landed at Aburatsu, Kyushu, Japan, in 1950 (Fig. 24).

During a fishing and marketing experiment (see section 5), *E. affinis* measuring 23 to 73 cm were taken by a

Table 25.—Size composition of catches of *Euthynnus affinis* in various areas of the Indian Ocean. (From Williams 1963, table 3.)

Area and author	Main size groups	Overall size
Australia		
Roughley (1951)	2.2-4.1 kg 5.4-6.6 kg	Up to 76 cm and 8.2 kg
East Africa		
Morrow (1954)	—	51-71 cm at 1.9-5.2 kg
Williams (1964)	1.0-2.2 kg 3.6-5.4 kg	40-78 cm at 1.0-7.3 kg
Madagascar		
Fourmanoir (1955)	—	Up to 80 cm
Seychelles		
Ommanney (1953)	45-65 cm Over 65 cm	43-87 cm at 1.0-8.6 kg
Somalia		
Ogilvie et al. (1954)	50 cm at 3-4 kg	Up to 79 cm and 6 kg

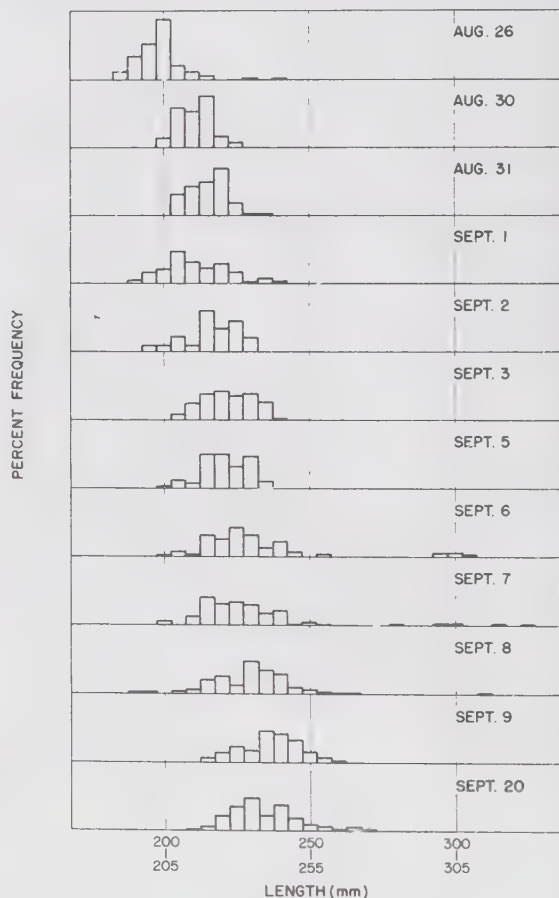


Figure 24.—Length frequencies of *Euthynnus affinis* landed at Aburatsu, Kyushu, Japan, in 1950. (From Yabe et al. 1953, fig. 1.)

modified purse seiner off Hong Kong. Two size groups were represented in the landings. The dominant group included fish from 50 to 73 cm long (2.5-7.0 kg) and the other less numerous group was composed of fish 38 to 44 cm long (1.2-2.5 kg) (Williamson 1970).

In the Philippines, the size of *E. affinis* taken by trolling by research vessels is shown in Figure 25. The fish ranged from about 30 to 80 cm and the length-frequency distribution showed a prominent mode at about 50 cm. Other commercial fishing methods capture much smaller *E. affinis*. Wade (1950a) reported finding *E. affinis* as

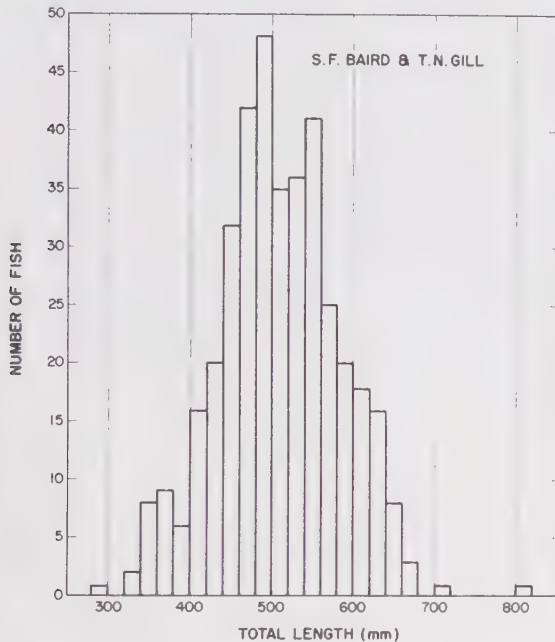


Figure 25.—Length frequency of *Euthynnus affinis* taken by trolling in Philippine waters, 1947-49. (From Ronquillo 1963, fig. 16.)

small as 40 mm in the fish markets in the Philippines. The length-frequency distribution of *E. affinis* taken in recent purse seine surveys near the Philippines (Rosenberg and Simpson⁶) is given below.

Length (cm)	Number	Percent
30	1	0.3
35	79	25.2
40	228	72.6
45	6	1.9
50	—	—

Elsewhere in the Pacific, size distribution of *E. affinis* taken by trolling around Hawaii and the Marquesas is shown in Figures 26 and 27, respectively. Length-weight relationships have been determined for *E. affinis* from various locations in the Indo-Pacific (Table 26).

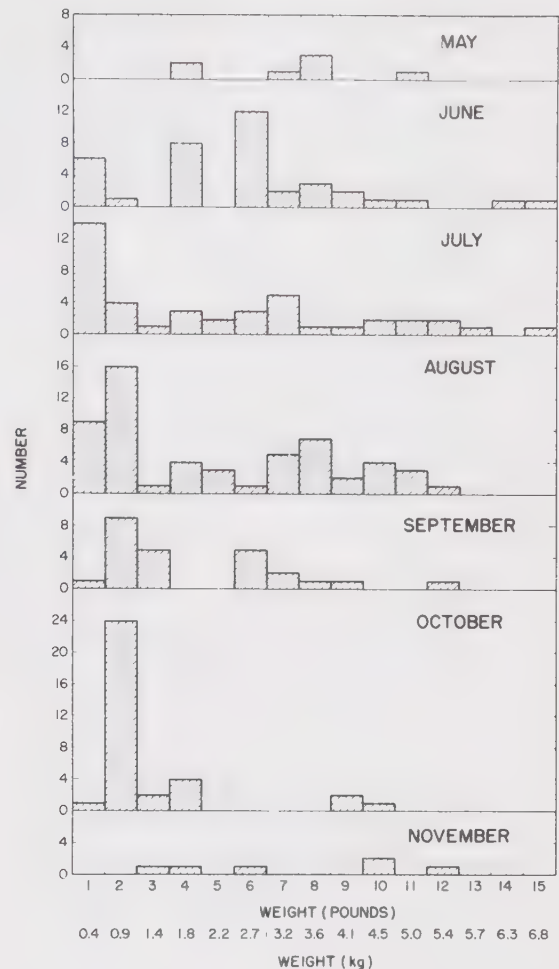


Figure 26.—Weight composition of *Euthynnus affinis* captured off Kaneohe, Oahu, Hawaii, by months, 1951-55. (From Tester and Nakamura 1957, fig. 6.)

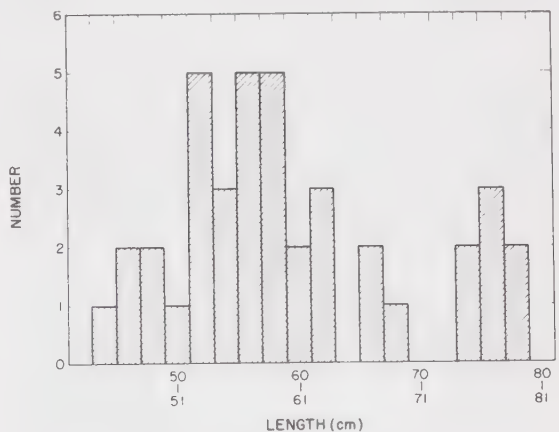


Figure 27.—Length frequency of *Euthynnus affinis* taken by trolling around the Marquesas Islands. (Data from files of Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.)

⁶Rosenberg, K. J., and A. C. Simpson. 1975. Pelagic fisheries development - trip reports chartered purse seine vessels. Regional. 9 February 1975 to 26 March 1975, voyage 3, 28 p. South China Sea Fisheries Development and Coordinating Programme.

Table 26.—Length-weight relations $W = aL^b$ of *Euthynnus*. Predictive equations were fit through logarithmic transformation of data (see Ricker 1973).

Species and locality	No. of fish	Size range of fish		a	b	Weight unit	Length unit	Source
		Weight	Fork length					
<i>E. affinis</i> (Indian Ocean)	10	1.81-5.22 kg (4-11.5 lb)	52-71 cm	0.0166	2.963	g	cm	Morrow (1954)
<i>E. affinis</i> (Indian Ocean)	201	—	12-58 cm	0.0137	3.0249	g	cm	Sivasubramaniam (1966)
<i>E. affinis</i> (Indian Ocean)	—	—	—	0.0138	3.0287	g	cm	Silas (1967b)
<i>E. affinis</i> (South China Sea)	226	—	—	0.08853	2.5649	g	cm	Williamson (1970)
<i>E. affinis</i> (Hawaii)	101	0.45-6.80 kg (1-15 lb)	—	0.0108	3.1544	g	cm	Tester and Nakamura (1957)
<i>E. affinis</i> (males) (Philippines)	203	—	34.4-81.0 cm	0.0334	2.83768	g	cm	Ronquillo (1963)
<i>E. affinis</i> (females) (Philippines)	165	—	33.1-65.2 cm	0.0211	2.94854	g	cm	Ronquillo (1963)
<i>E. alletteratus</i> (western Mediterranean)	325	—	—	0.0222	2.914897	g	cm	Rodriguez-Roda (1966)
<i>E. alletteratus</i> (eastern Atlantic)	—	—	—	0.0152	3.0	g	cm	Postel (1950)
<i>E. alletteratus</i> (Tunisia)	100	1.35-13.9 kg	473-1,015 mm	0.0163	3.0	g	cm	Postel (1956)
<i>E. alletteratus</i> (Florida)	343	0.23-8.39 kg	23.1-85.8 cm	0.00496	3.26314	g	cm	Beardsley and Richards (1970)
<i>E. lineatus</i> (eastern Pacific)	109	0.91-6.26 kg (2-13 lb 13 oz)	365-667 mm	0.01327	3.0817	g	cm	Klawe and Calkins (1965)

Euthynnus alletteratus

Juvenile *E. alletteratus* caught in the Sea of Marmara (from last week in August to mid-September) and the Dardanelles (mid-August to first week in October) in 1959 apparently were the first records of juveniles in Turkish waters (Demir 1963). The juveniles caught in the Sea of Marmara were slightly smaller (mode at 20 cm) than those taken in the Dardanelles (mode at 23 cm) (Fig. 28).

Rodriguez-Roda (1966) presented length-frequency distributions of *E. alletteratus* landed at Barbate and Tarifa, Spain, in 1963 and 1964 (Fig. 29). He smoothed the percentage frequency of the various length classes by the formula, $f = \frac{f_{n-1} + 2f_n + f_{n+1}}{4}$. The length distribu-

tions of the males and females were the same for both years. However, the length-frequency distribution in 1963 showed a single strong mode at 60 cm whereas the 1964 distribution showed two strong modes at 45 and 60 cm and a lesser mode at about 85 cm. It is of interest that the weight-frequency distribution, also smoothed by the formula given above, showed a single prominent mode at 4 kg in 1963 but in 1964 showed a mode at about 2 kg and another at about 9 kg (Fig. 30). Thus, in 1963 both the length- and weight-frequency distributions indicated only a single size group in the fishery but in 1964, three size groups were represented in the landings in terms of length, and only two size groups in terms of weight.

Postel (1955b) presented the length-frequency distribution of *E. alletteratus* taken in the eastern Atlantic off Senegal (Fig. 31). He stated that the length group from 30 to 45 cm were 1 to 2 yr old fish and those from 60 to 75

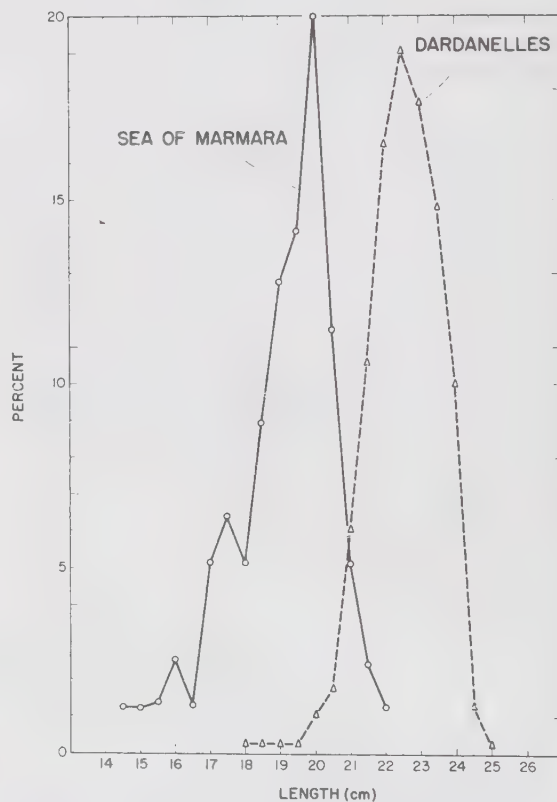


Figure 28.—Length frequencies of juvenile *Euthynnus alletteratus* from the Sea of Marmara and the Dardanelles. (From Demir 1963, fig. 2.)

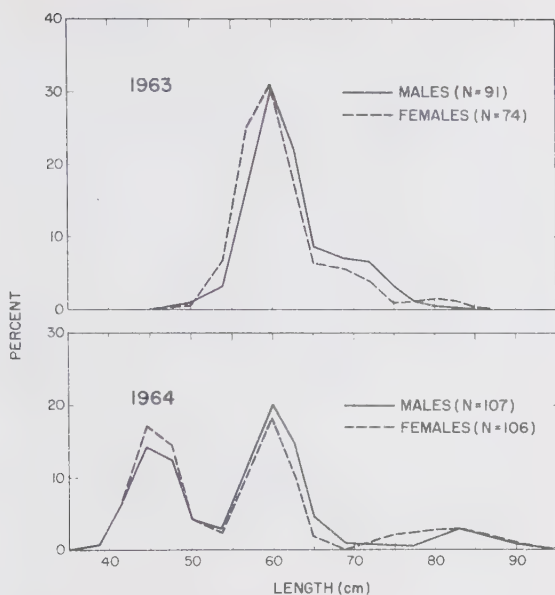


Figure 29.—Length frequencies of *Euthynnus alletteratus* landed at Barbate and Tarifa, Spain, in 1963 and 1964. (From Rodríguez-Roda 1966, fig. 6.)

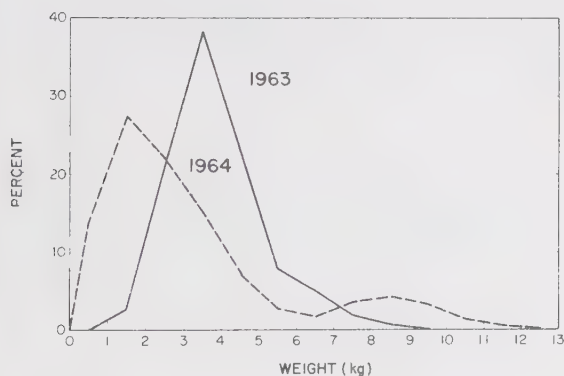


Figure 30.—Weight frequencies of *Euthynnus alletteratus* landed at Barbate and Tarifa, Spain, in 1963 and 1964. (From Rodríguez-Roda 1966, fig. 7.)

cm were 3 to 4 yr old. He noted that fish 45 to 60 cm long (2-3 yr old) were not found in the area off Cap Vert, Senegal. However, Marchal (1963) stated that *E. alletteratus* from 50 to 70 cm were found in normal proportions off the coast of Guinea.

The length-frequency distribution of *E. alletteratus* caught by sport fishermen on charter boats off Miami, Fla., is shown in Figure 32. In Figure 33 is shown the length-frequency distribution of *E. alletteratus* taken by commercial trolling between North Carolina and northern Florida. The length range of fish generally landed by the Miami sport fishery (Fig. 32) was from about 500 to 750 mm (de Sylva and Rathjen 1961). de Sylva and Rathjen noted that only a very few large or very small fish were taken and that fish larger than 620 mm were pre-

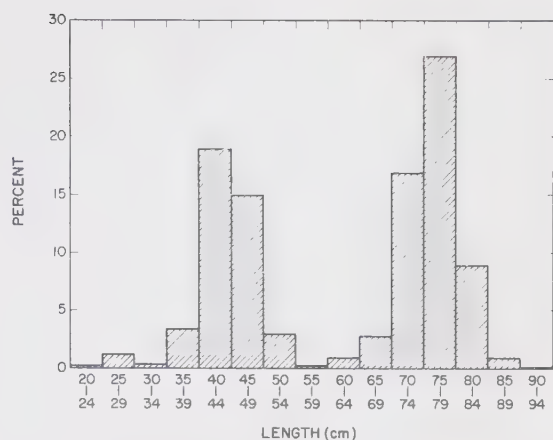


Figure 31.—Length frequency of *Euthynnus alletteratus* from Senegal. (Data from Postel 1955b.)

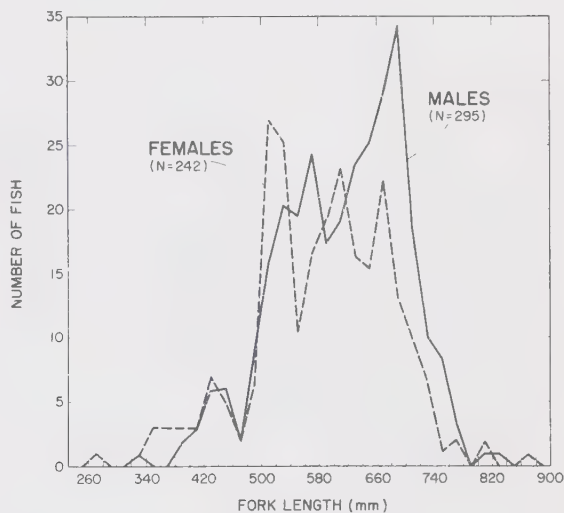


Figure 32.—Length frequencies of male and female *Euthynnus alletteratus* caught by anglers off Miami, Fla., September 1952 to August 1953. (From de Sylva and Rathjen 1961, fig. 1.)

dominantly males, possibly suggesting either a differential growth rate or mortality beginning at that size between the sexes. They also found that the *E. alletteratus* taken by commercial trolling between North Carolina and northern Florida were of similar size as those taken off Miami. However, they pointed out that the length-frequency distribution of the Miami sample showed a more even distribution of sizes while that of North Carolina-northern Florida was markedly leptokurtic. They suggested several causes for the disparity in the length-frequency distributions from the two areas, including the fact that the commercial trolling gear possibly selected a certain size range of fish by the use of only a certain range of hook sizes, as also suggested by Carlson (1952). Carlson indicated that the selectivity was possibly due to the loss of smaller fish caused by the hooks pulling free more easily. de Sylva and Rathjen

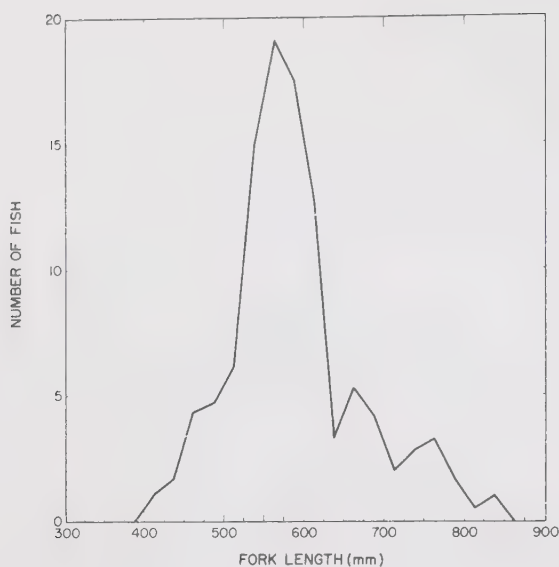


Figure 33.—Length frequency of 217 *Euthynnus alletteratus* caught by commercial trolling gear between North Carolina and northern Florida, July 1951. (From de Sylva and Rathjen 1961, fig. 2.)

(1961) also suggested that in the Miami sport fishery the anglers use a wider assortment of baits and artificial lures and because the angler is more careful in landing the fish, the hook is less apt to pull free.

Beardsley and Richards (1970) also presented length-frequency data of *E. alletteratus* caught in the sport fishery in southern Florida (Fig. 34). These fish were sampled at a Florida taxidermy firm during a period from September 1967 to September 1968. They indicated that because the fish was sampled at a taxidermy company the length-frequency distribution may be biased because usually only the largest fish caught are preserved and mounted. A comparison of the length-frequency data presented by de Sylva and Rathjen (1961) (Fig. 32) with that of Beardsley and Richards (1970) (Fig. 34), however, does not clearly indicate that larger fish were being selected.

The length-weight relationships determined for *E. alletteratus* from various localities are given in Table 26.

Euthynnus lineatus

The length-frequency distribution of *E. lineatus* taken between June 1972 and August 1975 in the Gulf of California and from Baja California to Ecuador is shown in Figure 35.

The length-weight relationship for *E. lineatus* computed by Klawe and Calkins (1965) is given in Table 26. The largest *E. lineatus* collected by Calkins and Klawe was a male 636 mm long which weighed 4.8 kg (10.5 lb).

4.14 Subpopulations

For various reasons, probably including the fact that 1) *Euthynnus* in general are commercially not very impor-

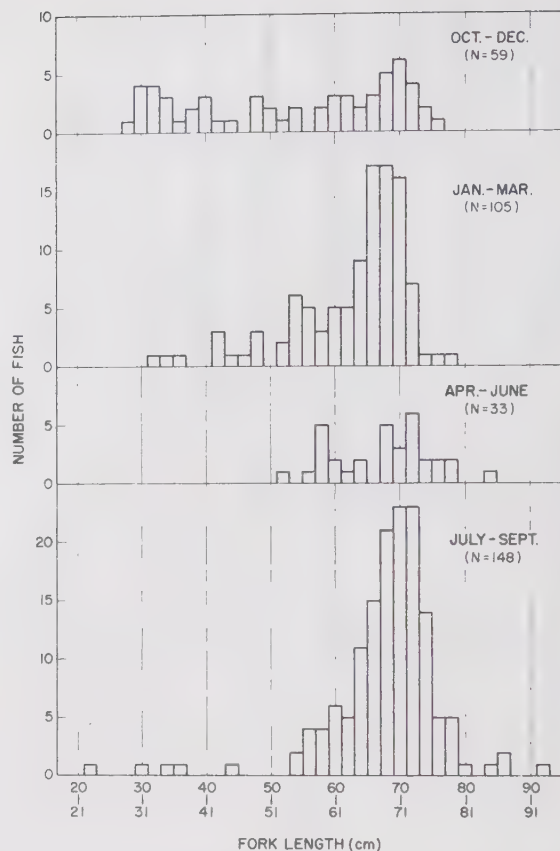


Figure 34.—Length frequencies by quarters of the year for *Euthynnus alletteratus* sampled from a taxidermy plant in south Florida from September 1967 through September 1968. (From Beardsley and Richards 1970, fig. 2.)

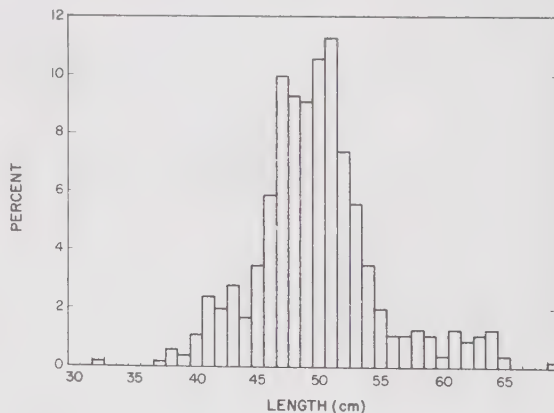


Figure 35.—Length frequency of *Euthynnus lineatus*. (Data courtesy of W. Klawe, Inter-Am. Trop. Tuna Comm., La Jolla, Calif.)

tant and 2) investigators had been concerned primarily with clarifying the species status in the genus, very little has been done to investigate the subpopulation problem within this group. Based on various published works on

meristic and morphometric characters of *E. alletteratus* in the Mediterranean and eastern Atlantic, Marchal (1963) concluded that two subpopulations existed in this area. He stated that the Senegal population extended at least from Cap Vert, Senegal, to Ghana and probably well beyond the tropical coast of west Africa. The Mediterranean subpopulation, which can be differentiated from the subpopulation off Senegal by meristic and morphometric characters, extends into the Atlantic south to Morocco and perhaps to as far north as the Bay of Biscay, France. In an earlier work Postel (1953) attempted to determine if the *E. alletteratus* that appeared in the cold season and the warm season off Cap Vert belonged to separate subpopulations on the basis of the number of spots on the pectoral region of the two groups of fish. Because of the wide variability of the number of spots the results were not conclusive.

In a preliminary study of the serology of tunas including *E. affinis*, Cushing (1956) indicated that it was probable that serological techniques could be applied profitably to the study of racial and specific variation in tunas. He stated that species differences existed among several species of tunas tested including *E. affinis*. In some preliminary experiments on two *E. lineatus*, it was found that the blood of this species could be differentiated from that of six other scombroids from the eastern tropical Pacific (Calkins and Klawe 1963). Other than these preliminary studies nothing has been done on subpopulation determination by serological methods.

4.2 Abundance and density (of population)

Probably because of the relative commercial unimportance of the species of *Euthynnus*, very few detailed studies have been made on the relative abundance of these fishes. Sivasubramaniam (1970) investigated the exploited stock of *E. affinis* along the southwest coast of Sri Lanka. He found a high degree of variability in catch rates of *E. affinis* within four subareas along the southwest coast which he attributed to seasonal changes in occurrence and to the schooling behavior of this species. He concluded that the best index of the relative density of *E. affinis* was an average taken from the mean catch rates obtained in the four subareas. The catch rate was given as the catch in pounds per operation or trip not exceeding 24 h. Sivasubramaniam (1970) found that the index of relative density was higher (35.3) in 1968 than in 1969 (31.1). He also indicated that the mean value of relative density obtained for the southwest subarea could indicate the relative strength of recruitment of *E. affinis* along the whole southwest coast. He noted that *E. affinis* are first recruited into the troll fishery in the southwest subarea along the southwest coast.

Sivasubramaniam (1970) estimated that a little over 600 tons of *E. affinis* were landed in 1969 on the southwest coast of Sri Lanka. These landings did not include those made by the nonmechanized boats. He noted that there is evidence of differential spatial distribution of *E. affinis* by size and that it could be possible to avoid capturing small fish by avoiding areas occupied by them. He

indicated that the annual yield of the fishery could be considerably increased by doing this.

Elsewhere in the Indian Ocean it has been recorded that *E. affinis* occurred in commercial quantities in Australian waters (Roughley 1951) and around Somalia (Ogilvie et al. 1954). Williams (1964) noted that there are large unexploited schools of *E. affinis* in east African waters and Morgan (1956) estimated that *Euthynnus* and *Sarda* represented about 0.5% of all fish by weight in the Indian Ocean.

Marchal (1963) reported that the manner of fishing and total catches of *E. alletteratus* have had no effect on the populations of this species. Rodríguez-Roda (1966) presented long-term landings data of *E. alletteratus* in the Spanish fishery covering the period from 1929 to 1964. The landings were given in numbers of fish and show wide annual fluctuations but no significant trends.

4.3 Natality and recruitment

4.3.1 Reproduction rates

See section 3.1.

5 EXPLOITATION

It was noted earlier that *Euthynnus* generally has little or no commercial value. In many localities it appears that the typical fishery for *Euthynnus* is a multispecies fishery. It is not very clear whether the *Euthynnus* or the other species of tunas are the main targets of these fisheries. *Euthynnus* usually schools together with other species of tunas, and sometimes nontunas, and the use of nonselective gear and fishing methods probably accounts for the mixed catches. However, there is some evidence of size-differentiated schooling habits in *Euthynnus*. In the Indian Ocean, it was found that small *E. affinis* tended to be found in pure schools but the larger fish were found to school with other species (Williams 1963). Williams also noted that in Madagascar, Somalia, Seychelles, Pakistan, Sri Lanka, and the west coast of India, *E. affinis* is the prime objective of fisheries and specific attempts are made to catch this species.

The FAO Yearbook of Fishery Statistics (FAO 1977) indicates that nine countries had landings of *E. affinis* between 1973 and 1976. In the Indian Ocean, the following countries showed landings: Maldives, Pakistan, Seychelles, Yemen (Arab Republic), and Indonesia; in the western Pacific: Indonesia, Malaysia, Papua New Guinea, and Philippines; and in the central Pacific: United States. Other sources (FAO 1974a, 1974b) showed that Bangladesh, India, Israel, and Sri Lanka also at one time had landings of *E. affinis*.

In the Atlantic Ocean and the Mediterranean Sea, the following countries had landings of *E. alletteratus* between 1973 and 1976: Angola, Bulgaria, Cyprus, Ghana, Ivory Coast, Mauritania, Morocco, Poland, Romania, Spain, United States, Venezuela, and Yugoslavia (FAO 1977). An earlier list (FAO 1974a) showed that Israel,

Liberia, and Turkey also at one time had landings of *E. alletteratus*.

Euthynnus lineatus landings for Panama and the United States between 1973 and 1976 are shown in the FAO Yearbook of Fishery Statistics (FAO 1977).

5.1 Fishing equipment

Silas (1967b) described the "multiple trolling" tuna fishery off the southeast coast of India (Gulf of Mannar). This is a multispecies fishery and in addition to *E. affinis*, a number of other species are taken. The vessels used in the fishery are known as Tuticorin-type boats which are small sailboats ranging in length from 8.2 to 10.4 m (27-34 ft). These vessels troll seven or nine lines and carry a crew of six or seven fishermen on the smaller boats and seven to nine fishermen on the larger boats. Brined *Sardinella* (*S. albela*, *S. gibbosa*, and *S. sirm*) are used almost exclusively as bait and only rarely are artificial lures used.

Other methods of fishing for *E. affinis* in the Gulf of Mannar include bottom-set nylon nets (150 mm mesh), shore seines, drift nets (pachuvalai) of 130-150 mm mesh, and longlines (Chacko et al. 1967). In the southern sector of the Gulf of Mannar, the drift nets are set in depths of about 30 m. The longline set is composed of up to 400 hooks baited with squid and the gear is set in depths of 25 to 40 m.

Off the southwest coast of India at Vizhingam, a tuna fishery is conducted almost exclusively by dugout canoes and catamarans (Bennet 1964). Including *E. affinis*, seven species of tunas are taken in this fishery. The other species are *Auxis rochei*, *A. thazard*, *Sarda orientalis*, *Thunnus tonggol*, *T. albacares*, and *Katsuwonus pelamis*. Bennet (1964) stated that *E. affinis* is one of the most important commercial species at Vizhingam. The principal fishing gears include cotton and nylon drift nets, hook and line, and occasionally shore seines. From July 1960 to October 1961, he noted that 71.4% of the landings of *E. affinis* were made by drift nets, 24.3% by hook and line, and only 4.3% by shore seines.

In the coastal waters of Sri Lanka, mechanized boats of 3.5-ton class and 11-ton class, in addition to the traditional outrigger canoes, are engaged in the mixed tuna fishery (Sivasubramaniam 1970). The fishing gear used includes drift nets, trolling lines, pole and line, longline, and beach seines (Sivasubramaniam 1966, 1970). In Pakistan the fishing gear or methods used are trolling, longlines, handlines, and beach seines (Qureshi 1952). In the Malagasy Republic, Comoro Island, east Africa, Somalia, Seychelles, and Australia the commonest fishing method for *E. affinis* is trolling with either natural bait or artificial lures. Handlines and longlines are also used in Somalia (Williams 1963).

In Japan no specialized fishery for *E. affinis* exists, apparently because consumer demand for this species is not great (Kikawa and staff 1963). Presumably, most of the *E. affinis* caught in Japan are taken incidentally with other species. Kikawa and staff (1963) stated that *E. affinis* are taken together with *Auxis*, juvenile *K. pelamis*,

T. albacares, and *T. thynnus*. In the coastal waters of Japan, *E. affinis* are taken mainly from small sailing and motorized vessels. They are also taken by pole and line.

In an attempt to develop a tuna fishery in Hong Kong, the Hong Kong Fish Marketing Organization offered to buy *E. affinis* at a special high price in 1967 and 1968. Two boats switched to tuna fishing using a modified purse seine method. About 16 t of *E. affinis* were landed in the 2 yr but the fish could not be marketed at a profit and the project was abandoned (Williamson 1970).

Warfel (1950) stated that the most productive method of catching tuna in the Philippines is the fish trap, called corral, or in Tagalog, baklad. The beach seine is the next most productive. Other methods used are a Philippine version of a purse seine called a talakop, trolling (sibid-sibid), and occasionally a drive-in net.

In Hawaii, *E. affinis* is taken incidentally in the live-bait pole-and-line *Katsuwonus pelamis* fishery and recreational troll fishery.

Euthynnus alletteratus

Like many of the fisheries for *E. affinis*, the fisheries for *E. alletteratus* appear to be multispecies fisheries. Along the coast of Tunisia in the Mediterranean, for example, Postel (1956) lists *T. thynnus*, *Sarda sarda*, *Auxis* sp., and *E. alletteratus* as species taken in specialized traps called madragues. Madragues are also used in the Moroccan fishery (Marchal 1963). The Tunisian fishery lands 400 to 500 tons and the Moroccan fishery 200 to 300 tons of *E. alletteratus* per year (Postel 1964).

Fisheries for *E. alletteratus* along the east coast of Africa are apparently not well developed (Marchal 1963). They are caught in beach seines in Senegal, the Ivory Coast, Ghana, and Angola. Off the Ivory Coast, *E. alletteratus* are also taken in sardine purse seines and in Angola they are also taken in traps similar to the madrague (Marchal 1963). On the islands of Sao Tomé and Principe, *E. alletteratus* are taken by a type of encircling gill net (Frade and Postel 1955).

In the western Atlantic and adjacent areas, Rivas (1951) stated that the flesh of *E. alletteratus* is good and of commercial importance throughout the West Indies. Chilton (1949) reported that for many years *E. alletteratus* has been caught in varying amounts along the Atlantic coast of the United States and along the coast of the Gulf of Mexico. Chilton's account of this species along the Atlantic and Gulf of Mexico coasts indicates that although *E. alletteratus* is frequently taken, and sometimes in fair amounts, no large-scale sustained fishery exists for this species in these areas. Mansueti and Mansueti (1962) reported on this species in Chesapeake Bay and stated that during 1951-61, *E. alletteratus* had been harvested commercially in pound nets and hand seines. However, the annual landings were minimal (less than 6 t per year). In addition to pound nets and hand seines, *E. alletteratus* in the western Atlantic has been taken by menhaden purse seines and trolling with artificial lures (Chilton 1949; de Sylva and Rathjen 1961).

Euthynnus lineatus were not fished commercially in the eastern tropical Pacific before 1972 except for the small numbers that were taken and sold fresh in the local markets of Latin American countries. This species is taken incidentally by gear used to catch other species of fish. They have been taken by tuna purse seines, by live-bait pole-and-line fishing, commercial and sport trolling, and by trolled handlines. They are taken by commercial tuna vessels of all sizes, from small albacore trollers to large purse seiners and by bait boats, and by Ecuadorian and Peruvian canoe and raft fishermen (Calkins and Klawe 1963). Since 1972 the following commercial catches of *E. lineatus* have been reported in the Inter-American Tropical Tuna Commission's yellowfin tuna regulatory area (data courtesy of Calkins⁷):

Year	Catch (tons)
1972	660
1973	1,845
1974	4,043
1975	582
1976	1,673
1977	1,195

5.2 Fishing areas

See section 5.3.

5.3 Fishing seasons

Euthynnus affinis

Off the coast of South Africa and southwest Australia, *E. affinis* occur and are fished during the southern summer when surface water temperatures are at a maximum (Williams 1963). In the Seychelles, the fishery is highly seasonal and takes place during the northwest monsoon (October-November to April-May), when the surface water temperature is highest (29°-30°C). In northern Somalia, the fishery is conducted during the northeast monsoon at the time of minimum sea-surface temperature. In Pakistan, west coast of India, and Sri Lanka, *E. affinis* is taken throughout the year with slight local seasonal variations (Williams 1963). Bennet (1964) found that good landings of *E. affinis* occur during the 8 mo from October to May and the period of low catches is from June to September (Table 27) in the Vizhingam fishery (southwest coast of India). Bennet observed that the period of low catches coincides with the southwest monsoon when the seas are rough and very little fishing effort is expended. In contrast to the generalized statement made by Williams (1963) on the seasonal nature of the *E. affinis* fishery in Sri Lanka, Sivasubramaniam (1970) described a somewhat more complex situation of the seasonality of the *E. affinis* fishery (Fig. 36). The seasonal picture around Sri Lanka is complicated by two

Table 27.—Monthly landings (kilograms) of *Euthynnus affinis* at Vizhingam, India. (From Bennet 1964, table 1.)

Month	1956	1957	1958	1959	1960	1961
January	12,091	8,929	5,725	6,130	4,360	8,436
February	8,827	3,970	10,843	2,737	15,998	16,825
March	6,198	25,761	8,022	8,022	15,501	24,384
April	8,444	10,446	1,957	4,498	4,623	32,236
May	6,151	4,131	3,602	7,105	11,192	27,775
June	—	3,937	3,086	1,501	2,290	1,259
July	—	13,405	—	567	510	290
August	324	402	—	11,952	5,663	10,072
September	—	—	19,072	26,957	7,067	21,999
October	4,514	5,394	25,580	9,499	81,026	22,537
November	26,675	16,267	15,462	20,560	34,969	—
December	12,451	2,621	32,753	5,009	22,569	—
Total	85,675	95,263	126,102	104,537	205,768	165,813

factors: the differential selectivity of the gear used (trolling and drift net) and variation in recruitment by size in the various areas around Sri Lanka.

Off east Africa, around the Comoro Islands and the Malagasy Republic, *E. affinis* is taken throughout the year (Williams 1963). *Euthynnus affinis* is present around the Philippines throughout the year but the highest catches are made from October through December and April through May (Warfel 1950). Around Japan, *E. affinis* is taken near the Izu Islands from May to November (Kikawa and staff 1963). Young *E. affinis*,

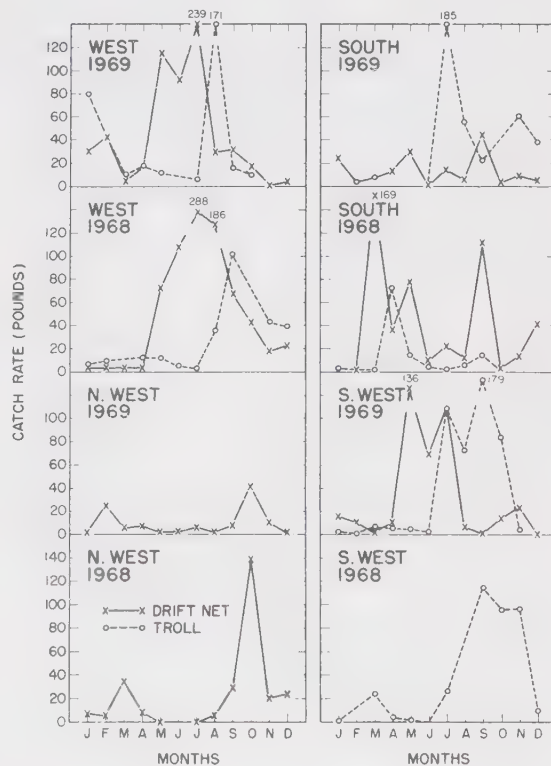


Figure 36.—Seasonal variation in catch of *Euthynnus affinis* around Sri Lanka. (From Sivasubramaniam 1970, fig. 4.)

⁷T. P. Calkins, Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography, La Jolla, CA 92037, pers. commun. March 1978.

15 to 25 cm long, have been caught near Aburatsu in southern Kyushu from August to October (Yabe et al. 1953).

The mean monthly landings of *E. affinis* at two ports in Kochi Prefecture, Japan, in 1973 and 1974 (Fig. 37) indicate that *E. affinis* are present throughout the year near Kochi. Because of the sparse data, the significance of the three peaks in January, May, and September is not clear.

In troll fishing conducted off the northeast coast of Oahu, Hawaii, from 1951 to 1955, Tester and Nakamura (1957) reported that no *E. affinis* were taken between De-

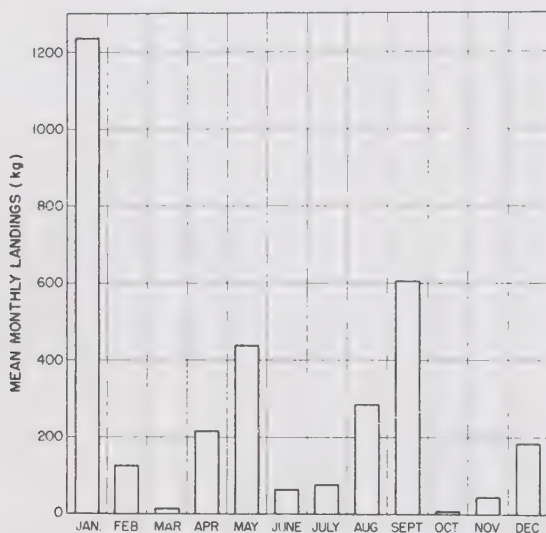


Figure 37.—Mean monthly landings of *Euthynnus affinis* in Kochi, Japan, 1973-74. (Data courtesy of T. Koto, Nansei Reg. Fish. Res. Lab., and S. Kikawa, Far Seas Fish. Res. Lab., Japan.)

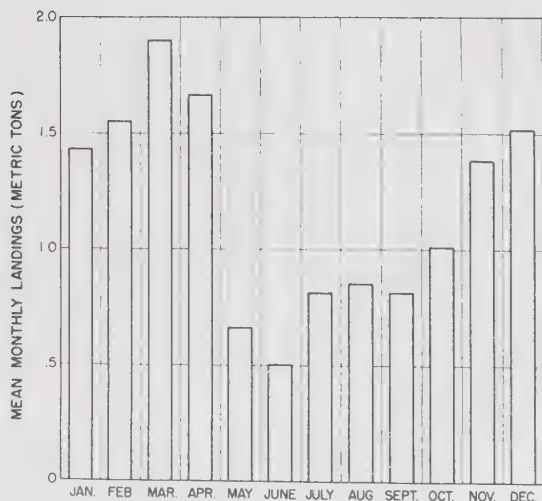


Figure 38.—Mean monthly landings of *Euthynnus affinis* in Hawaii, 1964-74. (Data from files of Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.)

cember and April. Their data showed a peak in the catch rate (catch per hour) in October. However, they cautioned that the fact that no *E. affinis* were taken from December to April cannot be regarded as significant since only a small number of hours were expended in fishing during that period. Welsh (1949) reported good catches of *E. affinis* during March, April, and May 1948 and during February and April 1949 in Hawaiian waters, including the same area fished by Tester and Nakamura (1957). The mean monthly landings of *E. affinis* in Hawaii from 1964 to 1974 indicate higher landings from October to April (Fig. 38). The results obtained by Tester and Nakamura (1957) and Welsh (1949) are not inconsistent with those shown in Figure 38. Thus it appears that around Hawaii, *E. affinis* may be less available from May to September and more available from October to April.

Euthynnus alletteratus

In the Gulf of Gabès, Tunisia, *E. alletteratus* is found sporadically throughout the year. Off the northern coast of Tunisia, it appears in the spring and disappears in the autumn (Postel 1964). In Morocco, Postel stated that *E. alletteratus* appears in May and disappears at the end of November. Data presented by Ben-Tuvia (1957) on the mean monthly landings of *E. alletteratus* during 1950 to 1955 in Israel (Fig. 39) indicate this species is caught throughout the year and that the landings peak in May and October. Rodriguez-Roda (1966) gave a summary of the fishing seasons and the months of peak catches for *E. alletteratus* in the various Spanish fisheries in the Mediterranean and the Atlantic (Table 28). The various seasonal peaks in the Mediterranean fisheries suggest that this species may make seasonal migratory movements.

Off the coast of Senegal in the eastern Atlantic, *E. alletteratus* arrive in large numbers in January-February

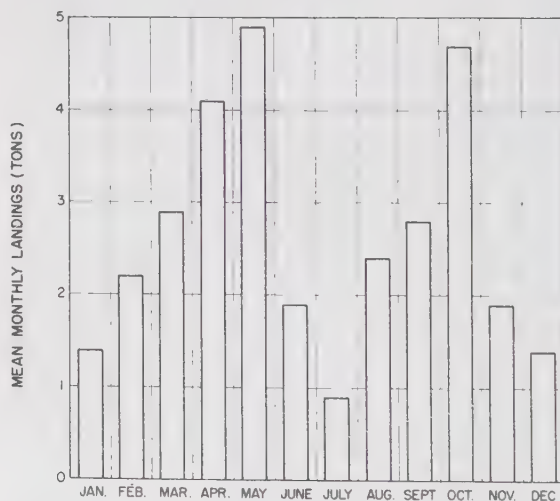


Figure 39.—Mean monthly landings of *Euthynnus alletteratus* from 1950 to 1955 in Israel. (From Ben-Tuvia 1957, table 3.)

Table 28.—Fishing seasons for *Euthynnus alletteratus* in Spain.
(From Rodríguez-Roda 1966, table 3.)

Region		Fishing season	Months of peak catches
North coast	Atlantic Ocean	Jan. to Dec.	Sept. and Oct.
Northwest coast		June to Dec.	Oct.
Southwest coast		Feb. to Dec.	Aug. to Oct.
Canary Islands		Jan. to Dec.	Dec. to Mar.
Southern coast	Mediterranean Sea	Jan. to Dec.	Sept. and Oct.
Southeast coast		Jan. to Dec.	Sept. and Oct.
Eastern coast		Apr. to Dec.	July to Oct.
Balearic Islands		Jan. to Dec.	May to July

and May-June (Postel 1955b). They are present all year in the region of Cap Vert (Marchal 1963). Off the Ivory Coast, Marchal (1963) stated that *E. alletteratus* are found throughout the year along the coastline but that the catches peak in February. He stated that *E. alletteratus* are caught in Angola starting in October, the catches peak in February and March, and become non-existent in May-June.

In the western Atlantic, Chilton (1949) suggested that *E. alletteratus* make seasonal migrations along the U.S. coast. In May and June they have been reported moving north to North and South Carolina and in August and September they have been caught along the coasts of New Jersey and New York. Observations made from September 1952 to August 1953 on anglers' catches landed at Miami, Fla., indicate that 87% of the catches were made from March through August including a peak in July (de Sylva and Rathjen 1961). de Sylva and Rathjen stated that there is evidence of a general drift of *E. alletteratus* out of the Miami area toward the south during the winter and that they occur further north along the coast during the summer.

Euthynnus lineatus

Euthynnus lineatus is taken throughout the year in all areas of its distributional range. Although information on the seasonal abundance is not very clear, Calkins and Klawe (1963) cited an Ecuadorian census of fishermen which indicated that *E. lineatus* was most abundant from May to September in the open coastal areas and from January to March in the Gulf of Guayaquil.

5.4 Fishing operations and results

5.4.2 Selectivity

The beach seines, principally used in the Sri Lanka fishery for *E. affinis*, are not size selective. Surface trolling, handlines, and longlines that are used in the Indian Ocean are also not selective (Williams 1963).

Calkins and Klawe (1963) stated that *E. lineatus* are taken by nonselective gear.

de Sylva and Rathjen (1961) suggested that the commercial trolling gear used to catch *E. alletteratus* may possibly be selective for a certain size range of fish (see section 4.13).

5.4.3 Catches

With the exception of the Philippines and Indonesia where a fair amount of *E. affinis* is landed, the species of *Euthynnus* are nowhere the basis of important large commercial fisheries. To illustrate the magnitude of the fisheries for *Euthynnus*, from 1965 to 1976 the total world landings for all the species fluctuated from 37,000 to 88,000 t (Fig. 40). In comparison, the annual world production of *K. pelamis* has ranged from 300,000 to 350,000 t in 1966-71 (Matsumoto 1974).

In Figure 40 is also plotted the total world production of *E. affinis* and *E. alletteratus* from 1965 to 1976. The world landings of *E. affinis* varied from 29,900 to 84,800 t annually and that of *E. alletteratus* from 4,600 to 9,500 t. *Euthynnus affinis* constituted 77.1 to 97.0% of the total for *Euthynnus* during this period. Only small amounts of *E. lineatus* have been reported in the statistics. It should be pointed out, however, that the world production of *Euthynnus*, as indicated by the statistics given above, is probably underestimated. It may happen that because only small amounts of *Euthynnus* are taken, they are lumped together with other species of tunas, or together with other miscellaneous species. Other problems associated with collecting catch statistics in the Indian Ocean are discussed in FAO (1973). Thus the figures for *Euthynnus* are probably not only underestimated but are also subject to inaccuracies.

The production of *E. affinis* from 1973 to 1976 in the Pacific and Indian Oceans is given in Table 29. As noted earlier, the Philippines and Indonesia have comparatively large fisheries for *Euthynnus*. The Philippines landings of *E. affinis* fluctuated from 9,447 to 24,000 t be-

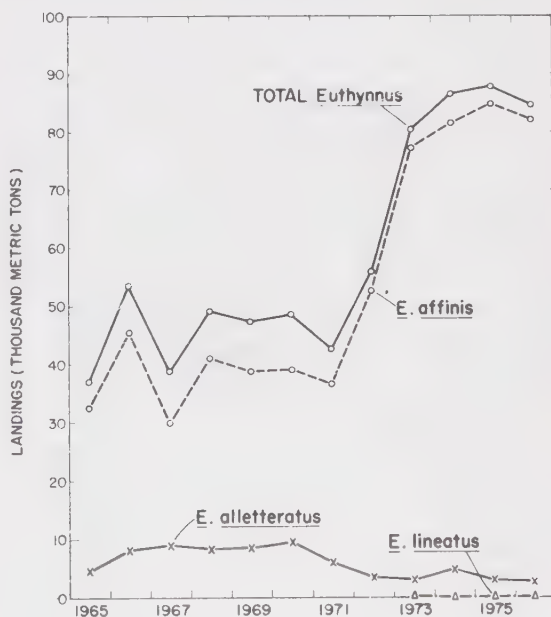


Figure 40.—World landings of *Euthynnus*. (Data from FAO 1974a, 1976, 1977.)

tween 1973 and 1976. The landings in Indonesia fluctuated between 31,600 and 41,616 t (Pacific Ocean) and 5,200 and 8,609 t (Indian Ocean) during the same period. Although the FAO Yearbook of Fishery Statistics does not show any landings of *E. affinis* in India from 1973 to 1976, according to Bennet (1964), 85.7 to 205.8 t were produced in Vizhingam, India, between 1956 and 1960 (see Table 26). In Hawaii, where *E. affinis* is taken incidentally in the pole-and-line fishery for *K. pelamis*, between 8.0 and 43.9 t were recorded during the 14-yr period from 1964 to 1977. In Japan, production figures for *E. affinis* are not readily available because they are combined with those of other species (Kikawa and staff 1963).

The world landings of *E. alletteratus* from 1973 to 1976 are shown in Table 30. It can be seen that only relatively small quantities of this species are taken in any of the fisheries. During the period from 1973 to 1976, the total annual production of *E. alletteratus* in the western Atlantic amounted to slightly over 500 t. In the eastern Atlantic, during the same period, the total annual

landings fluctuated between 1,967 and 4,285 t, and in the Mediterranean Sea they did not exceed 700 t during the same period.

Although the FAO Yearbook of Fishery Statistics does not show any figures for *E. alletteratus* from Tunisia, Postel (1964) reported that 400-500 tons are landed annually in Tunisia.

Calkins and Klawe (1963) stated that most of the landings of *E. lineatus* are probably made by small boats in Latin America and that they go unrecorded. They further noted that landings are sometimes recorded in Mancora, Peru, but it is not known what proportion they make up of the actual total landings even in the immediate area of Mancora. Tuna purse seiners sometimes inadvertently set on *E. lineatus* but these catches are dumped overboard. However, estimates of the amount caught have been recorded in the vessels' logbooks which indicate that amounts from 1 to 100 tons have been caught (Calkins and Klawe 1963). In years when large amounts of tuna are caught by setting on schools, as opposed to setting on porpoises, large quantities of *E. lineatus* are dumped overboard (Klawe⁸).

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Table 29.—Landings of *Euthynnus affinis* in metric tons. (From FAO 1977.)

Area	1973	1974	1975	1976
Pacific Ocean total	60,850	58,233	61,654	59,003
Indonesia	31,600	38,507	39,625	41,616
Malaysia	5,000	8,145	9,963	7,810
Papua New Guinea	250	250	30	100
Philippines	24,000	11,315	12,013	9,447
United States	0	16	23	30
Indian Ocean total	16,300	23,132	23,156	23,028
Indonesia	5,200	8,609	7,710	7,927
Maldives	1,000	800	400	1,000
Pakistan	9,600	13,113	14,470	13,575
Seychelles	300	350	250	200
Yemen (Arab Republic)	200	260	326	326
Total <i>E. affinis</i> landings	77,150	81,365	84,810	82,031

¹Estimated.

Table 30.—Landings of *Euthynnus alletteratus* in metric tons. (From FAO 1977.)

Area	1973	1974	1975	1976
Western Atlantic Ocean total	300	382	360	506
Poland	—	—	2	—
United States	0	9	1	5
Venezuela	300	373	357	501
Eastern Atlantic total	2,000	4,285	2,515	1,967
Angola	900	1,287	449	449
Bulgaria	0	—	8	—
Ghana	—	66	138	76
Ivory Coast	0	1,583	860	400
Mauritania	1,000	1,000	1,000	1,000
Morocco	0	46	14	32
Poland	—	6	—	—
Romania	100	297	46	10
Spain	—	—	—	—
Mediterranean Sea total	700	13	27	8
Cyprus	0	5	7	7
Morocco	0	5	0	—
Spain	700	—	—	—
Yugoslavia	0	3	20	1
Total landings	3,000	4,680	2,902	2,481

¹Estimated.

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A Night Handline Fishery for Tunas in Hawaii

HEENY S. H. YUEN

Introduction

Modern commercial fishing for tunas brings to mind large superseiners and longliners with complicated and costly equipment and gear. In contrast, the rapidly growing night handline fishery for tunas near the island of Hawaii is remarkable in its simplicity and effectiveness. This fishery catches bigeye tuna, *Thunnus obesus*; yellowfin tuna, *T. albacares*; and albacore, *T. alalunga*, on elementary gear, a hook and line.

The effectiveness of the method is demonstrated by its catch rate which is approximately two fish per hook per night on the average. In comparison, catch rates of Hawaiian longline vessels are on the order of 0.03 fish per hook per day (Otsu, 1954).

Because of its inexpensive requirements, this method of fishing seems like a promising method for the many financially impoverished island communities in the tropical Pacific Ocean to utilize a marketable resource of export value. Nevertheless night handline fishing for tunas is not a widespread practice.

ABSTRACT—Night handline fishing effectively catches tunas in localized areas. The fishery for tunas by this method in Hilo, Hawaii, experienced a rapid growth when high prices on the fresh tuna market and fast air delivery to distant cities made new markets for the catch available. The simplicity of the method and low cost of equipment makes it a promising method for island cultures of low technology to use for developing a fishery. The paper describes the fishing method and gear in detail.

To my knowledge, the only other place where this method is used is in the Philippine Islands. There, virtually all of the commercial yellowfin tuna catch is made on night handlines (Oswald¹). Even in Hawaii this technique is used only by fishermen on the island of Hawaii. Fishermen from the other islands in the State have not yet adopted it. The information in this paper may stimulate interest in handline fishing in other areas.

This report includes a brief history of the fishery in Hawaii, a description of the fishing method and gear, a description of the catch and its value, and a summary discussion. The data for this report were gathered in 1976. Minor changes in method and new fishing areas since then are incorporated in this report.

History

In 1976 night handline operations for tuna in Hawaii were made exclusively from Hilo (population 28,500). The following account of the origins of the fishery are from interviews of oldtimers in the fishing community of that city as written references were not found.

Immigrants from Okinawa are believed to have started the fishery. They went out at night to catch squid as they had done in Okinawa. Occasionally something large would strike and snap their lines. Upon checking with the native Hawaiians they learned that the strikes were probably made by large tuna. They subsequently equip-

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ped themselves with gear to catch the tuna.

The exact year when the fishery started is not known. The first Okinawans arrived in Hawaii in 1899 to work in the then burgeoning sugar industry (United Japanese Society of Hawaii, 1971). It took another 7 or 8 years, however, for the immigrants to reach large numbers. By 1911, 12,000 were living in Hawaii. Allowing for time to fulfill their contracts with the sugar plantations, I would guess that the fishery for squid started in the second decade of the 1900's.

In the early years of the fishery the boats were powered by sail; by the 1930's up to about 40 motorized boats were involved. Until World War II the fishery was primarily for squid. The incidental tunas caught were known as "ika-sibi" (squid-tuna in Japanese), the name by which the fishery is called today. Because the boats were too small to have the large fish on board and did not carry ice to chill the catch, these tunas were towed alongside the boat on the way to port. Consequently, the ika-sibi had a reputation for having poor quality and could not compete on the market with tunas caught on longlines.

The squid fishery stopped abruptly on 7 December 1941, with the Japanese attack on Pearl Harbor. Maritime restrictions prevented boats from fishing at night for the duration of World War II.

When the fishery was resumed after the war, three to four boats equipped with iceboxes targeted on the tunas. Until 1971 the tuna-oriented part of the fishery was limited to these few boats by the market for fresh tuna. The entire catch was sold on the island of Hawaii, which had a population of 55,000-63,000 during that period. By 1971 fresh tuna prices had increased enough to make air shipment of tunas to other markets economical. By 1976 the night handline fishing fleet had grown to about 30 boats, about half of which

¹E. Oswald, South China Sea Fisheries Development and Coordinating Programme, Makati, Rizal, Philippines. Pers. commun., 1976.

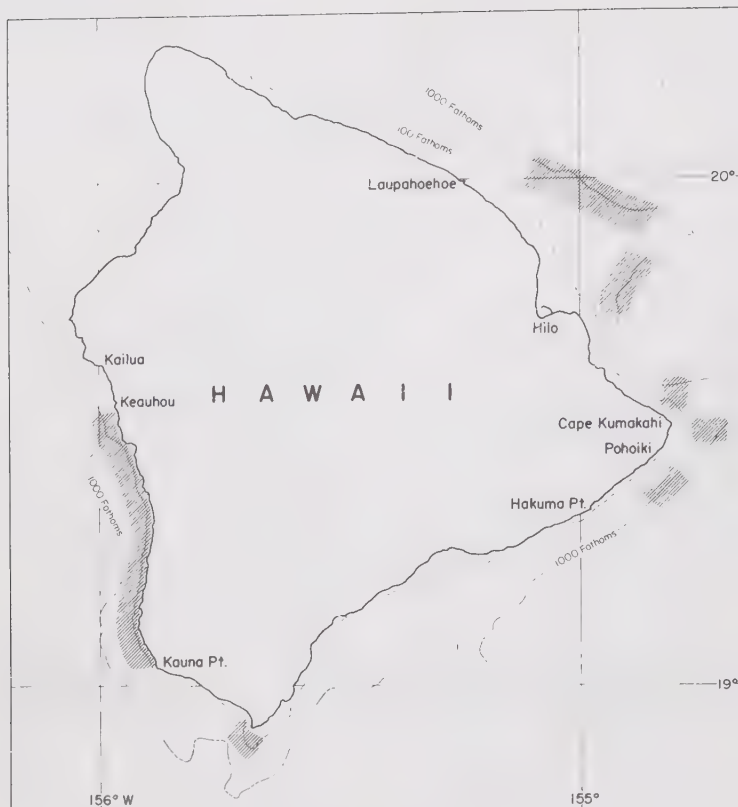


Figure 1.—Fishing locations of night handline fishery for tunas.

were part-timers. In 1977 over 40 boats were involved in the fishery from Hilo and about 10 or so boats were fishing from Kona on the west side of the island.

Fishing Operations

In 1976 the only fishing area was located 24–32 km (15–20 miles) north-east of the port city of Hilo on the east side of the island. Since then the fishery has expanded to other areas, the main ones of which are east of Hilo, south of Pohoiki, and the southern half of the west side of the island (Fig. 1). The areas fished are characterized by a marked increase in slope of the bottom beyond the edge of the shelf that joins the island. The depth of the shelf at the edge is about 400 m in the areas on the east side of the island and 200 m on the west side. During 1978 a few fishermen from Kona, a district on the western

side, successfully used night handlines in areas where the bottom is 4–5 km deep and relatively flat. They fished at night at sites where tuna were located during the day (Morioka²).

Geographic expansion of the fishery was accompanied by an expansion in the fishing season. In 1976 the handline fishing season was from July through December. This still holds true for the east side of the island. On the west side of the island the season runs from January to April.

The boats leave port to get to the grounds at sundown. Upon arrival the engine is turned off and a parachute is attached to the bow and lowered into the water as a sea anchor. Two above surface lights and one underwater light

are turned on. Some fishermen use just the above surface lights and some use just the underwater light but most of them use both types. Typically 25-W and 50-W incandescent bulbs are used for the above surface and underwater lights, respectively. Some fishermen use slightly brighter lights on moonlit nights.

The first fishing operation is to catch the squid, *Notodarus hawaiiensis*, for bait. Cross-sections of mackerel scad, *Decapterus pinnulatus*, or frozen squid, *Loligo opalescens*, roughly 1 inch (3 cm) wide, are used as chum. Squid are caught by angling and gaffing. The hooks are baited with mackerel scad by cutting off the tail so that the body of the scad is the proper length to fit on the shank of the hook and inserting the shank of the hook through the length of the fish starting with the cut end and ending at the mouth. A light line or wire attached to the proximal tip of the shank is wound around the fish to keep it from falling apart. This makes it possible to use the same piece of bait repeatedly despite the squid bites that are inflicted upon it. The baited hook is tossed out about 5 m and slowly pulled back to the boat. In this manner the hook is used not only to hook squid but also to lure the school of squid to within gaffing range of the boat.

A few fishermen prefer to gaff the squid exclusively. In this case the squid are lured to the boat by tossing out a whole scad hooked through the head with a fish hook and retrieving it in the same manner applied to the squid hook.

In the past, fishing for tuna began after 5–10 squid had been caught. Today most fishermen bait their tuna lines with mackerel scad and proceed with fishing while catching squid for bait. In fishing for tuna the baited hook is lowered to 20–30 m. The fishing line is tied to the boat with a restraining line to keep the hook at the desired depth. The restraining line is fairly heavy, about 18–34 kg (40–75 pounds) breaking strength, because it is intended to set the hook when the fish strikes. Three well separated hooks are fished: One at the bow, one amidship, and one at the stern. Some boats fish a hook at

²R. Morioka, Hawaiian Telephone Company, P.O. Box 1510, Kailua-Kona, Hawaii 96740. Pers. commun., 1978.

each corner of the stern and one amidship. None of the boats seems to fish more than three hooks at a time. While waiting for the tuna to strike, the fishermen continue to fish for squid.

On the western grounds where squid are scarce, squid fishing is often not done. The tuna hooks are baited with mackerel scad.

When a tuna strikes, the restraining line sets the hook and the fish is allowed to run until the outgoing line is slow enough to be handled. The fish is hauled by hand to the boat. At this point the fishermen differ in their techniques; some stun the fish and then gaff it; others stun the fish after it is on board. Fish are stunned with a blow on the head with a baseball bat or a wooden mallet. Recently many fishermen have resorted to killing the fish by shooting it in the head with a handgun when it is alongside the boat.

When there is a strike at least one of the other two lines is removed from the water as soon as possible to reduce the possibility of the lines tangling. This practice is not followed when the tuna is small enough to land quickly or during times when strikes are infrequent. Tuna strikes tend to be clustered and while it is possible to keep two lines with struggling fish from tangling, it is almost impossible to do so with three lines. The fishermen claim that tuna schools move away when the lines get tangled.

The fish are stored in iceboxes with a mixture of ice and seawater. Whenever the catch exceed the icebox capacity, excess fish are left on deck, covered with wet canvas or burlap, and cooled periodically with seawater. Departure from the fishing grounds is timed so that the fish can be delivered in time for the 7:00 a.m. auction. The newer and faster boats can thus stay on the fishing grounds longer.

Gear

Two sets of gear are used, one for catching squid and the other for catching tuna. There is much individual variation in the choice of materials and design of the gear. The following description is of the most typical gear.

Jigs and gaffs are used to catch

squid. A typical squid jig (Fig. 2) has a shank 25 cm long and eight prongs each of which is 5 cm long. Variation in the jigs occur in the number of prongs, which may be 6-10, and in the linear dimensions, which vary about 10 percent. The gaff (Fig. 3) is similar to the jig but with slightly longer prongs (7 cm). The handle is a straight piece of bamboo 1 m long and 2 cm in diameter at the larger end.

The tuna fishing gear (Fig. 4) consists of a hook, a leader, a lead weight, and a line. The hook (Fig. 5) is of a Japanese design (Tonkichi³ BKM #54). The leader is either seven-strand stainless, 227-kg (500-pound) test, wire or monofilament nylon of similar strength, sometimes braided for easier gripping. The leader length preferred by most is about 1 m but leaders 0.6-1.8 m are used. The weight (Fig. 5) is a lead tube of 227-397 g (8-14 ounces). The tube is bent at the middle about 30° to keep it from rolling around on the boat. A stainless steel rod is placed through the tube and its ends are fashioned into eyes to facilitate the attachment of line and leader. The favorite material for the lines is polypropylene rope either 0.95 cm (3/8 inch) or 0.79 cm (5/16 inch) in diameter. Lengths of the line range from 110 to 130 m. The fishing gear is coiled and kept in a square wooden box for easy handling.

Other equipment used by all boats are a parachute, lights, and a baseball bat or a wooden mallet. The parachute is 7.2 m in diameter and equipment surplus by the military. The lights, used for attracting squid, are of two types: Above surface and underwater.

³Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

Above surface lights are 25-W incandescent bulbs with polished metal reflectors. Usually two of these are used. The underwater light, usually one, is a 50-W incandescent bulb that has been waterproofed and weighted. Brighter bulbs are sometimes used for moonlit nights. The lights are powered by storage batteries. The baseball bat and wooden mallet are used for stunning fish.

A wide assortment of boats is used in the fishery. These range from 6-m (20-foot) fiberglass skiffs to an 18-m (60-foot) boat that fishes longlines during the off-season. The boats are usually manned by two men, but fishermen will often go out alone.



Figure 2.—Drawing of a hook for catching squid.

Figure 3.—A squid gaff.





Figure 4.—Photograph of a unit of handline gear.

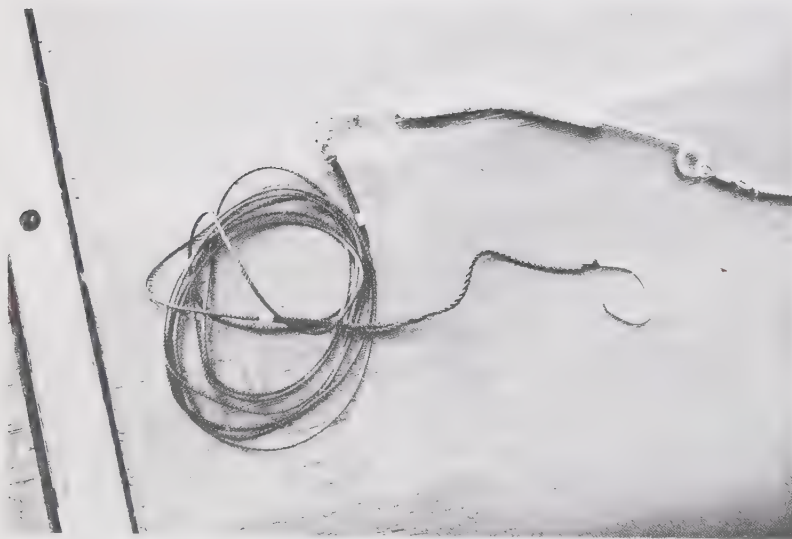


Figure 5.—Photograph of a hook, weight, and leader of handline gear.

Catch

Data on the catch, i.e., species, date of capture, number of fish, weight of each fish, and ex-vessel price for the years 1973-75 inclusive, were made available by Suisan Company, Ltd., which handled the sales of virtually all the catch of the night handline fishery at that time. On the sales records, weight is expressed in whole pounds. In the data analyses the pound was retained as the unit of weight. In the following presentation where weight is given to 0.1 kg, it is simply the metric equivalent of the original expression in pounds and was not meant to convey any implied precision.

The weight and value of the total catch are tabulated by species and year in Table 1. The annual weights and values for all tunas combined show a consistent growth of the fishery from 89,000 kg (196,000 pounds) to 155,000 kg (341,000 pounds) and from \$131,000 to \$328,000 over the 3-year period. The annual catches of the individual species, however, show a wide variation between years with 2 years having about the same catch and 1 year having a much greater catch. For the bigeye tuna, the catch in 1974 was almost twice those of the other 2 years. The catch of yellowfin tuna in 1975 more than tripled the catches of the previous 2 years. The catch of albacore, also high in 1975, was almost 60 times as great as the catch for the other years. The catch of squid reported in Table 1 is the amount sold at auction and represents the amount caught in excess of the squid used for bait.

Bigeye tuna caught in this fishery range in size from 2.3 to 128.3 kg (5-283 pounds). Frequency distributions of weight by year (Fig. 6) show that most of the bigeye tuna weighed less than 45.4 kg (100 pounds). In 1973 fish weighing 45.4 kg (100 pounds) or less comprised 87.7 percent of the catch; in 1974, 78.7 percent; in 1975, 71.7 percent. The size range of yellowfin tuna caught was from 2.7 to 125.2 kg (6 to 276 pounds). The size composition of this species varied considerably from year to year (Fig. 7). The median weight is a good example of the variability. It was 21.8 kg (48 pounds) in 1973, 81.6 kg (180 pounds) in 1974,

Table 1.—Weight and value of products of night handline fishery.

Species	Weight (t)			Weight (1,000 lb)			Value (\$1,000)		
	1973	1974	1975	1973	1974	1975	1973	1974	1975
Bigeye tuna	65.4	120.2	63.0	144.2	265.0	139.0	102.6	249.8	149.5
Yellowfin tuna	23.3	22.9	75.5	51.3	50.5	166.4	38.0	38.4	157.0
Albacore	0.4	0.2	16.1	0.8	0.4	35.5	0.5	0.2	21.0
All tunas	89.0	143.3	154.6	196.3	315.9	340.9	131.1	288.4	327.5
Squid	5.0	1.7	1.3	11.1	3.7	2.8	6.2	3.5	3.5

and 56.2 kg (124 pounds) in 1975. Albacore had a much more limited size range than the other species, 15.4-34.5 kg (34-76 pounds) (Fig. 8). There was one unusual individual of 3.2 kg (7 pounds).

The monthly distribution of catch for the years 1973 through 1975 (Fig. 9) show peak catches for yellowfin tuna and albacore during September and October, respectively. Bigeye tuna catches were more evenly distributed in time than the other species. October and September were the leading months.

Mention was made earlier of the high positive deviations in the catch of bigeye tuna in 1974 and yellowfin tuna and albacore in 1975. The bigeye tuna catch of 1974 and the yellowfin tuna catch of 1975 were compared with the catches of the other 2 years with respect to fish size and month to analyze the increase. More specifically, the average monthly catch in weight for each 4.5-kg (10-pound) weight class of 1973 and 1975 was subtracted from its corresponding catch in 1974 for bigeye tuna; the average monthly catch for each 4.5-kg (10-pound) weight class of 1973 and 1974 was subtracted from its corresponding catch in 1975 for yellowfin tuna.

The results for bigeye tuna (Fig. 10) show that for the months of July and August 1974 catch was slightly better than in the other years. The increase in catch was distributed fairly evenly over the remaining 4 months of the season. Contributing most to the 1974 increase was the December catch of 5.0- to 40.8-kg (11- to 90-pound) fish. Other major contributors to the increase in order of magnitude were the 68.5- to 104.3-kg (151- to 230-pound) fish in November and October, and the 27.7- to 45.4-kg (61- to 100-pound) fish in September.

The 1975 increase in yellowfin tuna catch was concentrated in the month of September (Fig. 11). Two-thirds of the increase in catch was made in September, 17 percent in October, and 15 percent in November. The largest increase in weight was in the 91.2- to 113.4-kg (201- to 250-pound) group. There was also a large increase in the 41.3- to 68.0-kg (91- to 150-pound) group.

Ages were assigned to the bigeye

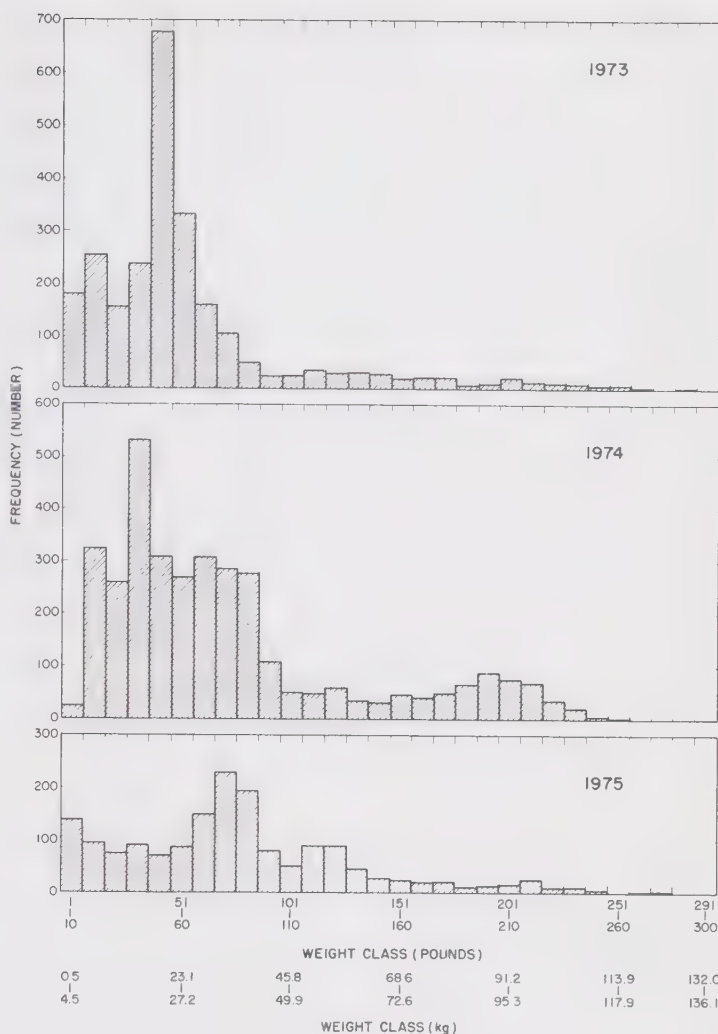


Figure 6. Frequency distribution of weights of bigeye tuna caught in the night handline fishery for tunas.

tuna catch based on size at age information of Shomura and Keala (1963) who assumed that spawning occurred in April. Since the fishing season has its peak half a year from the spawning season the fish were assigned mid-year ages. The catch curves constructed from the data (Fig. 12) indicate that recruitment is complete at age 2.5 years and possibly a year earlier as suggested by the data of 1973. Instantaneous rates of total mortality for fish between ages 2.5 and 7.5 years estimated from lines of least squares fit for 1973 and 1975 resulted in Z values of 0.73 and

0.90, respectively. Calculations were not made for the obviously anomalous year of 1974.

Discussion

The growth of the Hawaiian night handline fishery for tunas was dependent on two major factors: 1) The increased demand for fresh tuna of high quality for "sashimi" (a Japanese raw fish dish) and 2) the ability of modern transportation systems to speedily deliver the fish to markets as much as 6,400 km (4,000 miles) from the fishery.

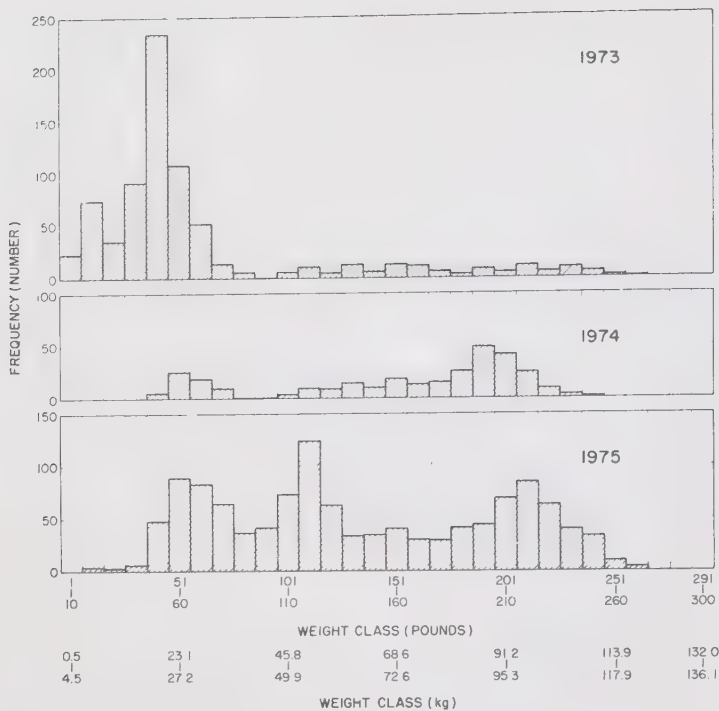


Figure 7.—Frequency distribution of weights of yellowfin tuna caught in the night handline fishery for tunas.

One of the problems of the fishery, which is handled expediently at the local level and accentuated by remote marketing, is the problem of "burnt" tuna. Tuna are labeled "burnt" when the normally dark red, translucent flesh is light pink, opaque, and slightly sour in taste. Burnt tuna is considered to be less desirable than normal tuna and sells at a lower price. "Burnt," however, is not a clear-cut condition, i.e., there is a continuum from very lightly burnt to heavily burnt. The burnt condition cannot be detected until the fish is dressed and the flesh exposed. Because tuna are transported whole to preserve their quality the burnt condition is not detected until after transportation expenses have been incurred. The problem is compounded when the seller who must accept the distant buyer's judgment of quality begins to doubt the integrity of the buyer.

The Honolulu Laboratory of the

National Marine Fisheries Service (NMFS) is now working to identify the cause of the burnt condition with the goal of preventing it. As an interim measure NMFS is also working on a field method to test for burnt tuna before the fish is sent to market.

The successful development of the night handline fishery in Hawaii depended heavily on knowledge of where the fish are going to be and the time of the year they are going to be there. Similar information will be required for development of night handline fisheries in other island communities.

Most of the Pacific island communities are not within the network of daily air transport schedules. Consequently, their tuna catches would have to be stored for later shipment and would be ineligible for the blue chip, fresh fish market. Two market options would still be open, however. The first, and probably less profitable of the two, is to

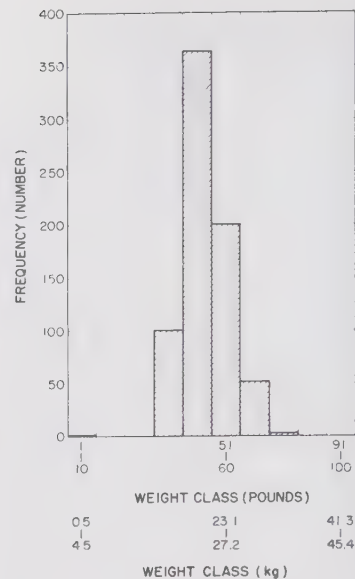


Figure 8.—Frequency distribution of weights of albacore caught in the night handline fishery for tunas.

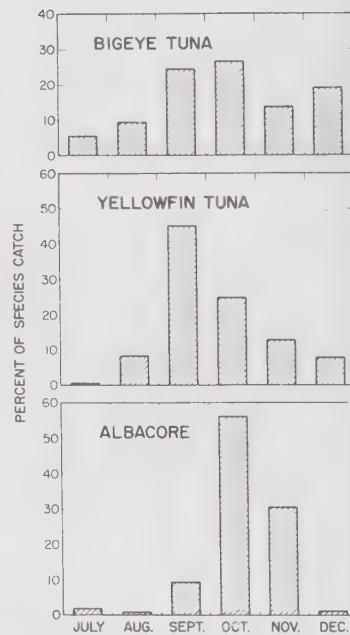


Figure 9.—Proportion of individual species total caught each month. Data of 1973 through 1975 combined.

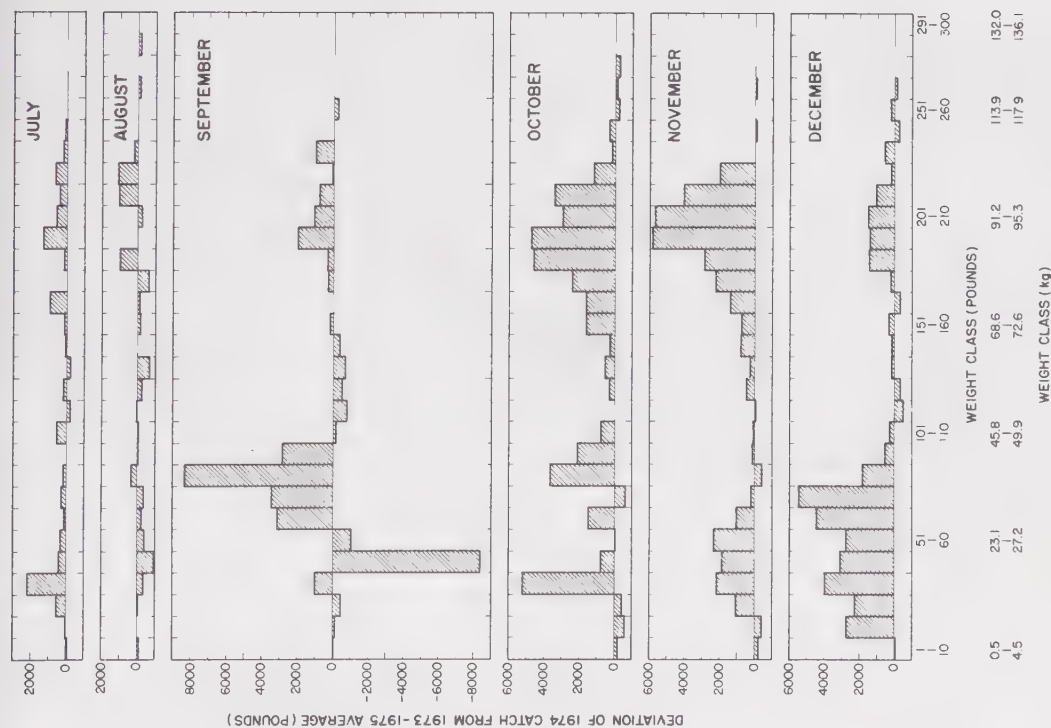


Figure 10. Deviations of the 1974 catch from the average catch of 1973 and 1975 for bigeye tuna.

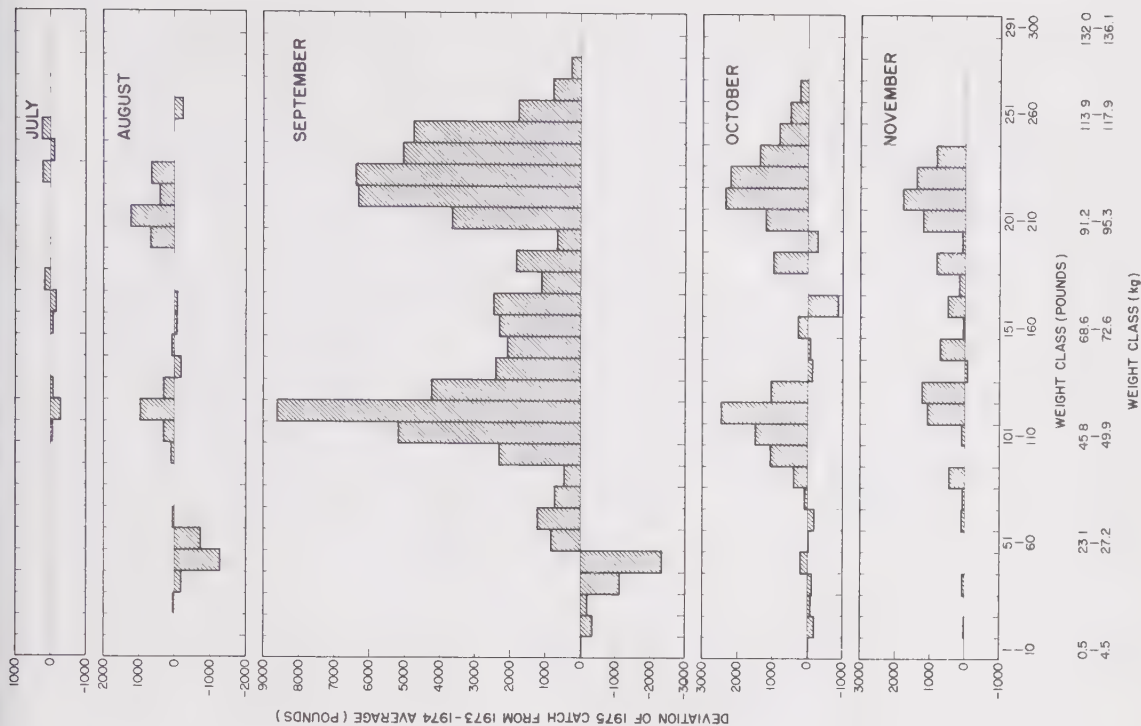


Figure 11.—Deviations of the 1975 catch from the average catch of 1973 and 1974 for yellowfin tuna.

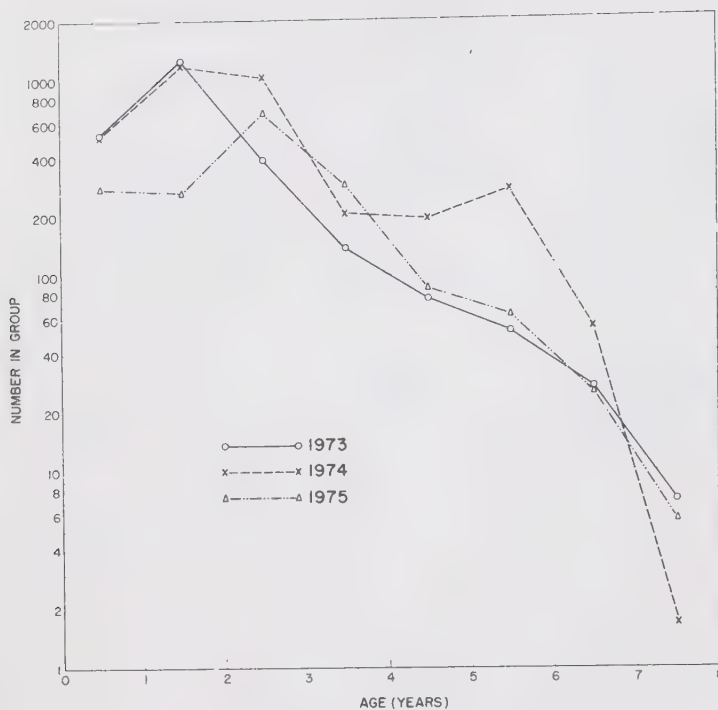


Figure 12.—Catch curve for bigeye tuna.

sell the catch to canneries. The second is to sell the fish on the sashimi market. The latter option is available if the flesh quality of the tuna is maintained by storing at -50°C .

Acknowledgments

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Agent in Hilo, made a conscientious review of the manuscript.

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